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Seed Quality of *Picea rubens* Sarg., *Abies balsamea* (L.) Mill., and *Abies fraseri* (Pursh) Poir. in Declining Spruce-Fir Forests of Eastern North America

By

Antonia L. Agmata

A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in the Department of Forestry

Mississippi State, Mississippi

December 1989

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December 1989

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by

Antonia L. Agmata

1989

Dedicated

to

Dr. Franklin T. Bonner

for his many contributions

to

Forest Seed Technology

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ALA

ABSTRACT

Antonia L. Agmata, Doctor of Philosophy, 1989

Major: Forest Resources
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Title of Dissertation: Seed Quality of Picea rubens Sarg., Abies balsamea (L.) Mill., and Abies fraseri (Pursh) Poir. in Declining Spruce-Fir Forests of Eastern North America

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ABSTRACT

Spruce-fir forests dominated by red spruce, balsam, and Fraser firs are now in a state of decline. Failure of seed to produce seedlings will affect the regeneration process of this valuable resource. Quality of seeds from these declining stands is virtually unknown, causing problems and uncertainty in the regeneration of the species.

This study was conducted to assess the quality of seed of declining spruce-fir stands in eastern North America using several seed quality criteria: cone size, seed yield, and physical and physiological seed characteristics.

Variation in seed quality was highly significant among trees within populations in all three species and less variable among populations and collection years. Seed quality of red spruce varied greatly in a poor seed year but varied little in good years; balsam fir showed the opposite; and Fraser fir quality did not vary significantly. Physical

seed characteristics were highly correlated with geographic locations. Stand characteristics could not be used to predict seed quality.

The variations in seed quality found among and within seed lots could not be described as extreme. The variation that did exist, however, could be related to different geographic locations.

No apparent seed quality impairment was observed among all seed lots. There was no strong evidence present for association between seed quality and elevation of collection sites, hence no influence of airborne pollutants on seed quality can be inferred.

TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS v

ABSTRACT vii

LIST OF TABLES.....xi

LIST OF FIGURES xiv

INTRODUCTION 1

LITERATURE REVIEW - Forest Decline.....3

A. Definition 3

B. Extent of Damage 4

C. Symptoms/Injury 8

D. Possible Causes 11

Impact on Regeneration 18

A. Seed Production (Stands and Trees).....18

Natural variation.....18

Effects of pollution and forest decline.26

B. Flowering and Pollination 28

C. Seed Germination 32

D. Seedling Development 34

MATERIALS AND METHODS.....36

Site Selection 36

Cone Collection 37

Seed Extraction, Cleaning, and Upgrading...39

Sampling and Test Procedures for Physical Seed Characteristics.....39

Sampling and Test Procedures for Physiological Seed Characteristics.....43

(continued)

TABLE OF CONTENTS (continued)

Page

Statistical Analyses.....48

RESULTS 49

Picea rubens Sarg.....49

Abies balmasea (L.) Mill. 75

Abies fraseri (Pursh) Poir. 96

DISCUSSION 118

Seed Quality Variations.....118

Seed Quality Relationships.....122

Prediction of Seed Quality.....124

SUMMARY AND CONCLUSIONS 125

Seed Quality Differences Among Populations 125

Seed Quality Relationships 126

Relationship to Stand and Tree Decline 127

APPENDIX 129

LITERATURE CITED 153

LIST OF TABLES

Table		Page
1.	Collection sites of three forest species studied	38
2.	Mean diameter and length of red spruce cones, 1987-1988	50
3.	Yield of filled seeds per cone of red spruce, 1986-1988	51
4.	Mean weight of filled seeds and fresh seedlings of red spruce, 1986-1988	52
5.	Mean length of embryo of red spruce seeds, 1986-1988	54
6.	Mean red spruce germination and peak value, 1986-1988	56
7.	Red spruce mean daily germination and germination value, 1986-1988	57
8.	Mean leachate conductivity of red spruce seed lots, 1986-1988	59
9.	Correlations among physical characters of red spruce seed lots	69
10.	Correlations between physical and physiological characters of red spruce seed lots	70
11.	Correlations of red spruce seed quality to stand characteristics	71
12.	Correlation between red spruce seed quality and stand location	73
13.	Regression equations that predict seed quality of red spruce	74
14.	Embryo length, seed and seedling fresh weight of balsam fir, 1987-1988	76
15.	Percent normal germination, peak value, and mean daily germination of balsam fir, 1987-1988	78

(continued)

LIST OF TABLES (continued)

Table		Page
16.	Germination value and leachate conductivity of balsam fir, 1987-1988	80
17.	Correlations among physical characters of balsam fir seed lots collected in two year....	86
18.	Correlations between leachate conductivity and other physiological characters of balsam fir.....	90
19.	Correlations between physical and physiological characters of balsam fir, 1987-1988.....	91
20.	Correlations between quality of seed and characteristics of balsam trees (seed source)..	93
21.	Summary of regression analysis of full model equation of balsam fir seed quality.....	94
22.	Correlations between seed quality of balsam fir and stand locations.....	95
23.	Mean percent filled and resin-filled Fraser fir seeds, 1986-1987 97	
24.	Mean weight of 1000-Fraser fir seed, embryo length, seedling fresh weight, 1986-1987..... .98	
25.	Mean percent normal germination, peak value, mean daily germination, and germination value of Fraser fir, 1986-1987.....101	
26.	Mean leachate conductivity of Fraser fir, 1986-1987 102	
27.	Correlations between physical characteristics of Fraser fir seed lots, 1986-1987.....111	
28.	Correlations between physical and physiological characters of Fraser fir seed lots.....112	
29.	Correlations between quality of seed and stand characteristics of Fraser fir.....	114
30.	Correlations between seed quality of Fraser fir and stand locations.....	116

(continued)

LIST OF TABLES (continued)

Table Page

31. Summary of regression analysis of full model equation of Fraser fir seed quality.....117

LIST OF FIGURES

Figures — Page

1. Flow chart of activities involved in seed extraction and conditioning.....40

2. Germination responses of Picea rubens Sarg. to accelerated aging.....60

3. Top view of a two-way thermogradient table showing germination responses of Picea rubens Sarg. seed lots collected in 1987.....62

4. Top view of a two-way Thermogradient table showing germination responses of Picea rubens Sarg. seed lots collected in 1988.....63

5. Relationship between 1000-seed weight and embryo length of Picea rubens Sarg. collected in (a) 1986, (b) 1987, (c) 1988.....65

6. Relationship between embryo length and seedling fresh weight of Picea rubens Sarg. collected in (a) 1986, (b) 1987, (c) 1988.... 66

7. Relationship between 1000-seed and embryo length of Picea rubens Sarg. collected in (a) 1986, (b) 1987, (c) 1988..... 67

8. Germination responses of Abies balsamea (L.) Mill. to accelerated aging.....81

9. Top view of a two-way thermogradient table showing germination responses of Abies balsamea (L.) Mill. seed lots collected in 1987.....83

10. Top view of a two-way thermogradient table showing germination responses of Abies balsamea (L.) Mill. seed lots collected in 1988.....84

11. Relationship between 1000-seed weight and embryo length of Abies balsamea (L.) Mill. collected in (a) 1987 and (b) 1988.....87

12. Relationship between embryo length and seedling weight of Abies balsamea (L.) Mill. collected in (a) 1987 and (b)1988.....88

(continued)

LIST OF FIGURES (continued)

Figure — Page

13. Relationship between 1000-seed weight and seedling fresh weight of Abies balsamea (L.) Mill. collected in (a) 1987 and (b) 1988.....89

14. Germination responses of Abies fraseri (Pursh) Poir. to accelerated aging test.....103

15. Top view of a two-way Thermogradient table showing germination responses of Abies fraseri (Pursh) Poir. seed lots in 1986.....105

16. Top view of a two-way Thermogradient table showing germination responses of Abies fraseri (Pursh) Poir. seed lots in 1987.....106

17. Relationship between 1000-seed weight and embryo length of Abies fraseri collected in (a) 1986 (b) 1987.....108

18. Relationship between embryo length and seedling fresh weight of Abies fraseri (Pursh) Poir. collected in (a) 1986 and (b) 1987.....109

19. Relationship between 1000-seed weight and seedling fresh weight of Abies fraseri (Pursh) Poir. collected in (a) 1986 and (b) 1987.....110

INTRODUCTION

Spruce-fir forests form an important ecosystem in eastern North America. Dominated by red spruce (Picea rubens Sarg.), balsam fir (Abies balsamea (L.) Mill.), and Fraser fir (A. fraseri (Pursh) Poir.), these forests cover 21 million acres along the Appalachian Mountains. Pure red spruce and red spruce-balsam fir mixtures grow at low elevations throughout Nova Scotia, New Brunswick, and southeastern Canada, and in the northeastern United States (Eyre 1980). As the spruce-fir type occurs southward, Fraser fir replaces balsam fir in the ridges and peaks of the southeastern mountains, while red spruce grows more abundantly at the lower elevations (Dull et al. 1988).

Red spruce and balsam fir are of major economic importance as timber resources in the northeast (Hertel 1985). In the southeast however, red spruce and Fraser fir are primarily valued for their hydrologic and aesthetic significance. They protect the mountain tops (Speers 1974), maintain water quality and regulate stream flow (Franklin 1974). Simultaneously, spruce-fir forests provide beauty to the Appalachian Mountain Trail and serve as a seed source for the Christmas tree and ornamental nursery industry (Dull et al. 1988).

But spruce-fir forests are now in a state of decline. Recent evidences of growth reduction, extensive forest dieback, and mortality are fully documented (Johnson and Siccama 1983; Hertel et al. 1987, 1988; Weiss et al. 1985;

Dull et al. 1988), and numerous hypotheses relating potential causal factors have been proposed. At present, there is a lack of knowledge about the regeneration of stands damaged by forest decline. Any silvicultural system that utilizes natural regeneration has two key elements: seed supply and seedling survival (Franklin 1968). Absence of these features in the spruce-fir ecosystem will stop the spruce-fir regeneration process. Although successional trends can be determined only over long study periods, some immediate studies can indicate potential problems in stand regeneration. Heavy cone or seed crops is a common phenomenon in trees under stress (Rudolf et al. 1974). Unfortunately, there is a lack of good data on the quality of seed produced under these conditions and on the impact these seeds could have on stand succession. It was therefore the objectives of this work to assess the quality of seed crops from trees in declining stands by examining cone and seed characteristics, seed yields, and germination responses; and to determine the relationships of seed quality with other seed and mother tree characteristics and geographic locations of seed sources. This work is an integral component of cooperative efforts to preserve spruce-fir ecosystems in the Eastern United States. These efforts are funded by the Environmental Protection Agency (EPA) and managed by the USDA Forest Service through the Eastern Spruce-Fir Research Cooperative.

LITERATURE REVIEW

Forest Decline

A. Definition

Decline is one of the three categories of plant diseases described by Manion (1981). He defined decline as a "complex disease condition caused by the interaction of biotic and abiotic factors that produces a gradual deterioration of a tree or stand, typically ending in mortality." Cowling (1986) expanded the decline concept from trees and forests to a larger scale by using the term "regional decline" to refer to any regionally widespread decrease in the health or vigor of forests. Thus, tree decline means a decrease in health of a single tree species on a regional scale; and forest decline is a decrease in health involving more than one species on a regional scale (Kulp 1987). However, Hyink and Zedaker (1987) argued that since all living organisms undergo a common natural phenomenon of culminating annual increment followed by decreasing growth rates, there should be a basis for determining expected growth, because below this growth the organism is declining. As Schroeder and Kiester (1989) stated, "decline is a negative trend beyond the natural bounds of variability".

B. Extent of Damage

Assessment of abnormal forest changes and ascribing causes to these changes are extremely difficult since forests are complex, long-lived ecosystems that may respond slowly and subtly to stress (Franklin et al. 1987, Klein and Perkins 1987, Woodman and Cowling 1987). Visible foliar symptoms were first observed in Norway spruce (Picea abies (L.) Karst. in the German forests in 1970. They spread to many European countries in a decade (Henrichsen 1986, Nilsson and Duinker 1987, Huettl 1989). The yellowing and loss of needles that occur at high elevations on acidic soils (Zottl and Huettl 1986, Rehfuess 1987) is similar to the symptoms recently noticed in the United States. They were first observed in the mixed conifer forests of the San Bernardino National Forest in California in 1950 (Miller 1983), then the spruce-fir forests in eastern North America (Hertel 1988). Several later reports indicated decreased growth rate and significantly increased mortality in 20- to 25-year-old red spruce at numerous locations throughout the northern and southern Appalachian Mountains (Siccama et al. 1982, Johnson and Siccama 1983). According to Cowling (1985), in this century alone at least five regional forest declines occurred in Europe and 13 in North America. Based on the European Economic Community survey, forest damage has extended to eight countries other than the Federal Republic of Germany (Brandt 1988), and most of the damaged species

are valuable timber species (Postel 1984, Nilsson and Duinker 1987, Brandt 1988).

In the past 20 years, high elevation red spruce and fir forests in large areas from Maine to North Carolina have shown visible symptoms of injury, decreased radial growth, and increased mortality (Johnson and Siccama 1983, Bruck 1987). A 100 percent mapping of dead spruce and fir in forests of the Northeast revealed a decreasing gradient in damage from west to east, with several mountains in the Adirondacks having 50 percent or more standing dead trees. The most extensive red spruce mortality occurs on the northwest-facing side of Whiteface Mt. (Johnson et al. 1984). Dead trees were fewer in the Green Mountains than in the Adirondacks, but more than in the White Mountains (National Acid Precipitation Assessment Program 1989). When red spruce and balsam fir stands were surveyed in 1984, Weiss et al. (1985) found that mortality had been greater for red spruce and balsam fir (1.3 percent/year) than for other associated species. Fir mortality (2.3 percent/year) exceeded that of spruce (0.5 percent/year) (Hertel 1988).

Similar decline trends were also found in the spruce-fir forests of the southern Appalachian Mountains. Based on a National Acid Precipitation Assessment Program (NAPAP) (1989) report red spruce mortality increased markedly above 1000 meters where a higher proportion of older trees were present. Severity of decline appeared to be related to

aspect, as the greatest degree of spruce mortality occurred above 1000 meters on the northwest aspect (Johnson et al. 1984). Furthermore, red spruce decline was more severe above cloudbase; a decrease of live spruce of about 40 to 70 percent has occurred on Whiteface Mountain since the mid 1960's (Siccama et al. 1982, Scott et al. 1985). Decline intensity in spruce-fir forests was positively correlated with elevation (Hertel 1985). In a recent survey of spruce-fir decline in the southeast (Dull et al. 1988), overall mortality for red spruce and Fraser fir was 8 percent and 67 percent, respectively.

In the Northeast, the most recent decline has been occurring for 25 years at elevations over 800 m. Foliage injury and needle loss of red spruce and balsam fir were significantly greater at higher elevations than at lower elevations (Friedland et al. 1985). There has been a 50 percent or greater reduction in number of trees over the past 25 years at elevations above 880 m in the Adirondack, White and Green Mountains. Between 1964 and 1986, a reduction of 60 to 70 percent of basal area was observed at Whiteface Mt. (Hertel 1988).

Extent of damage in the southeast varies; red spruce crown vigor decreased over the past years at Black Mountain and the Great Smoky Mountain Park (GSMP), but not at Mt. Rogers. The decrease in crown vigor was more pronounced at low elevations and in stands dominated heavily by Fraser fir (Zedaker et al. 1987, Hertel 1988). Dead trees were

found high on Mt. Mitchell and GSMP (21 percent of the total spruce-fir in the area), but Roan Mountain had higher mortality (45 percent). Other high elevation forests in the southeast (North Carolina, Tennessee, and Virginia) had less than 30 percent dead trees. Only 10 and zero percent dead trees were mapped in West Virginia and Mt. Rogers, Virginia, respectively, suggesting that the latter stands are more vigorous and healthy (Hertel 1988).

The percent of dead basal area increased with elevation for both red spruce and Fraser fir (Hertel 1988). The latter died markedly at elevations over 1920 m beginning in the early 1960s (Bruck 1988), and severe damage is evident on west-facing slopes of the higher peaks (Bruck and Robarge 1986). For instance, on Mt. Mitchell damage and ring-width suppression is worst on west-facing slopes, and almost half of the red spruce and Fraser fir were dead by 1987.

General growth decline based on basal area increments of trees across New England was found to be independent of elevation from sea level to 1,100 m. These growth rate declines were generally less severe and abrupt than for the above-cloudbase forests (Hornbeck et al. 1986). Reduction in radial growth in low-elevation, dominant and co-dominant red spruce was unexpected, for it is a second growth phenomenon not consistently present in old-growth stands (Hertel 1988). Similarly, the extent and rate of decline of shortleaf pine (Pinus echinata Mill.) under 16 inches

d.b.h. in the southeast has increased by 30 to 50 percent over the past 30 years, and annual mortality of pine growing stock has increased by 77 percent (Sheffield et al. 1985).

The extent of forest decline in the northeast and southeast is well-reported but not well-explained. Thus, no clear directional change has been detected for balsam fir populations (Hertel 1988); no relationship has been found between direction or steepness of slope and red spruce foliar damage (Donnelly et al. 1985); and decline of high elevation stands is not always correlated with stand basal area or tree age (Johnson and McLaughin 1986).

C. Symptoms/Injury

According to Kramer and Kozlowski (1979), a tree may be considered healthy when all of its physiological processes are fully functional, and it is relatively free of insect and disease pests. In contrast, in declining trees or forests physiological processes are malfunctioning, which leads to a significant decrease of overall biomass per unit area over time. As with individual trees, an entire species may be experiencing a net decrease in biomass per unit area over time (Kulp 1987).

The earliest symptoms of forest decline to be noted were reduction of tree height and diameter growth, followed by degeneration of the root systems, discoloration and size

reductions in foliage, dieback of twigs and branches, and with prolonged severity, tree mortality (Manion 1981, Ciesla 1987). Decline symptoms vary widely; some are host-specific, appearing in just one species (Cowling 1985), but others may cover several species within a region, causing random symptom distribution patterns (Hyink and Zedaker 1987).

Crown deterioration is the most visible symptom of forest decline. Crown conditions have been divided into classes: class 1 - needle loss from zero to 10 percent and class 2 - needle loss from 10 to 50 percent (Hertel 1988). Severe foliar damage and more abrupt decrease in growth rate occurred at elevations where the forests are bathed in clouds nearly 50 percent of the time (Kulp 1987). Foliar symptoms, however, differed from site to site. In the southern Appalachians and at lower elevations in Maine, discoloration and needle loss occurred from the inside of the crown outward, and from bottom to top (Johnson and Bruck 1985), both are similar to the symptoms observed in West Germany (Jagels 1986). According to Johnson et al. (1984), crown condition (foliar thinning) and growth reductions have been found to be the most important indicators of poor red spruce health in the southern Appalachians. The typical dieback from the top and the outside, i.e. discoloration and death of the newest needles and outer tips of branches from top to bottom of the crown (Siccama et al. 1982), was observed in red spruce in the

high elevation sites in New York and New England. Evans (1986) proposed a mechanism of initial injury-causing apical dieback in red spruce at high elevation. Twig injury and necrosis occurs on 1st-year twigs that retain injured or necrotic needles, and have zero bud enlargement (Evans 1986). This tip dieback is followed by loss of fine roots and increased mortality, often due to secondary fungal infections and reduced stand basal area (Kulp 1987).

The development of "stork nests", common in flat-topped trees over 100 years old, is now observed in young stands (25 to 30 years). Further, adventitious buds on the upper side of young branches of Norway spruce and white fir (Abies concolor (Gord. and Glend.) Lindl.) are more common in declining stands (Schuett and Cowling 1985). "Storknesting" and foliar symptoms in red spruce along the Maine coast were similar to Norway spruce symptoms in Central Europe (Jagels 1986).

Smaller ring-widths were evident in red spruce, balsam fir, and Fraser fir at 980 to 1577 m in Central West Virginia and Virginia (Adams et al. 1985). The occurrence of decreased ring-widths, which started after 1965, was usually abrupt. However, the appearance of the first unusually small ring-width did not occur at the same time in each tree, but small ring-width increment continued with no indication of recovery (Adams et al. 1985). Consequently, decrease of total basal area increased with

elevation, and the pattern was consistent with site quality (Zedaker et al. 1987).

The most severe symptom of decline is extensive mortality of red spruce, balsam fir, and Fraser fir within their natural range.

D. Possible Causes

All forest trees continually experience natural (abiotic and biotic) stresses during their lifetime. Most of these stresses vary in intensity diurnally, seasonally, annually, or for longer periods, and several can occur at a time (Kulp 1987); but the cause (or causes) in all cases remain to be conclusively identified (USDA Forest Service 1986). According to Klein and Perkins (1988), a variety of anthropogenic causal factor complexes interacting with natural events and processes induce stresses in forests that culminate in declines of individual plants and of ecosystems. This assumption was shared by Pitelka and Raynal (1989), as they speculated that decline results from multiple stresses that affect the physiological processes and health of forests, and that the relative contribution of any single stress varies from site to site.

Earlier, however, the USDA Forest Service (1986) and Woodman and Cowling (1987) were able to classify stress into six factors: competition among trees and other vegetation; weather extremes (Hertel 1988, Kulp 1987, Blank 1986, Rehfuess 1987) such as drought (Adams et al. 1985,

Johnson and Siccama 1983, Scott et al. 1985, Wargo 1985), unseasonal heat or cold (Friedland et al. 1985, Hamburg and Cogbill 1988), and high winds (Bruck and Robarge 1986); soil nutrient deficiency or excess that could disturb the nutritional balance; biological stress factors, including viruses, bacteria, and fungi; changes in site quality caused by human activities such as logging, overtapping in case of sugar maple (Acer saccharum Marsh.) (Wargo 1985), controlled burning, physical disruption and consequent erosion or depletion of nutrients in soil; and anthropogenic stresses such as pollutants (toxic, acidic, nutrient altering or growth altering chemicals in air, cloud water or precipitation) (Jagels 1986), soil compaction (Wargo 1985), mishandling of transplant seedlings, man-caused fires, and careless use of chemical pesticides (Woodman and Cowling 1987; USDA Forest Service 1986). Nicholas et al. (1987) have suggested an additional factor: normal growth dynamics of stands that have reached their carrying capacity.

Acid deposition, accumulation of heavy metals (Scott et al. 1985) and natural processes have been considered as causes for the growth reduction of red spruce in lower elevations (Hornbeck et al. 1986), while the balsam woolly aphid Agelges piceae (Ratz.) has caused the greatest mortality in Fraser fir (Busing and Clebsch 1988, Zedaker et al. 1987). Natural site disturbances, i.e. fir waves, may have affected basal area of balsam fir, but not red

spruce (Scott et al. 1985). Furthermore, damage caused by wind, snow, fire, drought, and some damage caused directly by air pollutants are also readily identified, but in some recent declines, even experts cannot diagnose the cause of specific injuries (Hertel 1988). Because of the geographic extent of the observed growth rate changes, and the large variability in site quality, stand age, and stand dynamics from site to site, regional rather than local stresses are more likely to be responsible for the decline. However, the roles of stand age, climate, insects, and diseases in the decline syndrome are not completely understood (Brandt 1988). In the early part of the decline syndrome, Manion (1981) suggested a sequence of three steps. First: predisposing stresses weaken a tree or forest by chronic exposures to severe climate and nutrient deficient soils. Other elements are air pollution and genetic make-up of trees (Manion 1985). Second: inciting stresses, such as insects or drought, are usually short term in nature, but severe enough to cause significant tree injury. Third: contributing stresses (or secondary causal factors) such as insects, fungi, viruses, and other tree pests act over a long period, often leading to tree death.

Crown deterioration and reduced growth are also influenced by the natural processes within the tree itself. Early induction of heavy cone crops in two fast growing Picea glauca (Moench) Voss provenances caused apparent loss of potential growth (Teich 1975). Excessive seed

production and associated crown deterioration of yellow birch (Betula alleghaniensis Britt.) and white birch (B. papyrifera Marsh.) were documented in detail in 1967 and 1968 in Ontario by Gross (1972). He concluded that excessive fruiting caused reduction of terminal and diameter growth of yellow birch. Heavy cone crops are known to reduce growth of conifers from 12 to 40 percent (Chalupka et al. 1975, Tappeiner 1969). Heavy flowering in balsam fir in New Brunswick reduced its foliage weight by 27 percent over that of the previous year (Morris 1951). In Douglas-fir (Pseudotsuga menziesii Mirb. Franco), Ebell (1971) has shown that girdling as a method of inducing cone production reduced carbohydrate concentration in shoots of all ages, growth and number of new shoots, and number of developed buds per shoot. He also confirmed that adverse effects will occur if girdling is conducted at the wrong time, and increases in abortion rates in the existing crop may occur when it is done repeatedly (Wheeler et al. 1985). Eventually, cone production stops in damaged stands, but, the dynamics of changing seed quality are not known.

Air-borne chemicals or air pollutants are frequently reported as factors affecting decline in forests. They are considered important (or potentially so) in the following examples (Cowling 1985): decline of pines in the San Bernardino Mountains in California; white pine (Pinus strobus L.) mortality in the eastern United States; Europe's "Waldschaeden"; red spruce-fir decline; decline in

growth of yellow pine (Pinus echinata Mill.) in the southeastern United States; and the recent symptomatically distinct decline of sugar maple in the northeast United States. Among the most severe instances of forest dieback are those reported in eastern Europe, where mortality is attributable to high sulfur dioxide concentration from point sources of industrial activity (Paces 1985). Scientists generally agree that air pollutants are among the primary causes of forest decline in Europe (Schuett and Cowling 1985, Huettl 1989). The Government of Switzerland and most of its public for example, consider air pollution to be the causal agent of their forest damage (Hinson 1987).

Although acidic precipitation or air pollutants were suspected to be the proximal cause due to syncrony of appearance of decline symptoms in different species and regions, not all declines were caused by a single factor (Rehfuess 1987). Regional air pollution was documented to be responsible in the visible decline of mixed conifers near the Los Angeles basin in California (Miller 1983). Strong relationships between diameter growth and sulfate deposition estimates were found for jack pine (Pinus baksiana Lamb.), red pine (Pinus resinosa Ait.), and sugar maple when deposition gradients from Minnesota to Michigan were studied (Shifley 1988). Recently, air pollutants and acidic deposition were seen in the high-elevation spruce-fir forests of the Appalachian chains (MacKenzie and El-

ashry 1988). According to Dull et al. (1988), high elevation forests in the mountain areas theoretically receive more atmospheric deposition than the surrounding forests of the lowlands; thus, wet deposition increases as elevation increases because of more cloud cover, precipitation, and deposition of snow that may be more polluted than rain. They also added that cloud water deposition is likely to be significant at high elevations because of the frequent immersion of mountain peaks and the presence of wind-driven clouds. Similarly, dry deposition should be greater at higher elevations because of higher wind speed, high relative humidity, and greater canopy surface areas. Wind-driven cloud droplets together with water-borne pollutants are deposited on the leaves and needles of mountain trees. Thus, cloud water interception contributes more sulfur and nitrogen to the forest than does wet and dry deposition (Mohnen 1988).

There are three primary pollutants in the United States (Congress of the United States 1985) and elsewhere : sulfur oxide, nitrogen oxide, and hydrocarbons. When these pollutants are carried by wind, they are transformed to secondary pollutants such as ozone and air-borne fine particles like sulfate and nitrate. High acid deposition results when sulfur and nitrous oxides return from the atmosphere to the earth's surface in rain, snow, fog, or dew, or as dry particles and gases. Dry deposition predominates close to the emission source, and wet

deposition predominates in distant areas. Both dry and wet depositions contribute to the total acidity received by the ecosystems, including soils (Bruck 1988), as these two processes are estimated to deposit equal amounts annually in the eastern United States (Congress of the United States 1985); however, acid deposition from precipitation is greatest in the northeastern United States (Council for Agricultural Science and Technology 1984). Cloud impaction in the Appalachian Mountains appears to increase with increasing latitude and elevation, and a significant altitudinal gradient exists for pollution-related ions in clouds with higher concentration at or near cloud base (Mohnen 1988).

Ozone has been reported by Skelly et al. (1987) as being the most phytotoxic air pollutant occurring in eastern North America. Growth of agricultural crops and forest trees were found to be significantly reduced by this chemical. Ozone is not known to have any beneficial effects on plant physiological functions (Kulp 1987), and it reduces photosynthesis in black oak (Quercus velutina Lam.) and red oak (Quercus rubra L.), slash pine (Pinus elliottii Engelm.), ponderosa pine (Pinus ponderosa Dougl. ex Laws.), eastern white pine, and sugar maple (United States Environmental Protection Agency 1986). Some mountain-top forests in the Appalachian Mountains may experience higher average daily ozone exposures than adjacent lower elevation forests (Kulp 1987). Ozone

concentration is higher in summer and lower in fall and winter months (Mohnen 1988).

Impact on Regeneration

A. Seed Production (Stands and Trees)

Natural variation. A thorough knowledge of cone and seed characteristics is particularly essential for sound forest management (Baumgartner et al. 1984). Studies with conifers in general suggest that vigorous, dominant, and large crowned trees are the best seed producers, and that open-grown stands produce better seed than dense stands (Fowells and Schubert 1956). These authors concluded that size and frequency of cone crops were both correlated with tree diameter, and number of seed cones was found to be most significantly correlated with tree height. Payandeh and Haavisto (1982) found that cones from intermediate trees initially had twice as many seeds as those from dominant or codominant trees, but dispersed their seeds at a greater rate. Similarly, Varnell (1976) reported that slash pine conelet and cone yields showed a weak correlation with d.b.h., tree height, percent of live crown, and tree age. He added that the number of seed per cone was not related to cone yields per tree or percentage of sound seed. Cone and seed parameters, however, are influenced by genetic and environmental factors (Fatzinger et al. 1980). In black spruce (Picea mariana (Mill.)

B.S.P.) for example, seed production is limited by an environmental gradient (Black and Bliss 1980). Variation in the number and dimension of cones, seed yield, weight of 1000-seed, and laboratory germination percent among trees of white spruce (Picea glauca (Moench) Voss) is mostly genetically controlled (Rubanik and Parshina 1978). According to Park and Fowler (1984), significant differences among female parents with respect to seed weight, percent germination, and seedling height are due to additive genetic and maternal effects. Variation in seed yield among trees (Nienstaedt and Teich 1972) and cone characteristics within the species (Cabala 1982) are characteristics of the genotype. Seed quality of balsam and Fraser fir, which is extremely variable from year to year and often in the same year from different geographic origins (Heit and Natti 1969), is influenced by both genetic and environmental influences.

According to Safford (1974), a good maturity index for red spruce cones is a shining brown color. A comparable index for Fraser fir is a brown cone color that occurs in early fall (Franklin 1974). Other indices are browning of cone bracts, and an embryo length that is more than 90 percent of the embryo cavity length (Ryynanen 1982). Cabala (1982) found tremendous variations in cone length (6.23-12.18 cm), seed yield (0.3-8.4 seed per cone), 1000-seed weight (1.3-9.4g), germination (5.75-98.84 percent), and percent blind seed (0.95-83.50 percent), among 63 Norway

spruce populations and 77 parents, but not much differece in cone diameter (2.20-2.94cm). The number of cone scales and the ratio of fertile to sterile cone scales are characteristics of a species (Bramlett 1974). Stoehr and Farmer (1986) concluded that 37 percent of the variances in cone size, seed yield, and germination properties of black spruce clones were accounted for by the differences among clones, and 19 percent by ramets within clones. Clonal variances for number of seed per cone and percent filled seed were 31 and 23 percent of the total variance, while ramets accounted for 18 and 13 percent, respectively. Variation in germination percent of filled seed was 67 percent due to clonal differences, while only 18 percent was associated with ramets. Verheggen and Farmer (1983) confirmed that both clones and ramets within clones accounted for a substantial amount of variation in germination percent (23-56 percent for all seed at 20°C), filled seed percent (23-59 percent), number of seed per cone (14-49) and cone size (1.4-2.4 cm^3). Cone size was only weakly correlated (r=0.44) with number of seed per cone.

In Pinus radiata D. Don., cone dimensions, number of scales, and mean seed weight were all found to show significant clonal repeatabilities within sites, confirming the genetic control of these characters (Burdon and Low 1972). Cone volume and mean seed weight were about one-third less at the phosphate-deficient site than elsewhere.

Number of scales varied little between sites. The only important clone-site interactions appeared to reflect differences between clones in response to the phosphate deficiency. Hence, they claimed that cone size and seed weight differ widely between natural populations owing to their environmental plasticity. When balsam fir stands were fertilized, no appreciable differences occurred in the N, P, K, Mg, Ca, and Fe of seed, and germination remained the same. However, the general quality of seed from fertilized trees was superior to that of seed from the unfertilized trees (Sheedy 1974).

The between-provenance variation was investigated for four seed characters of Taxus baccata L. in England: seed weight, speed of germination, rate of germination, and seedling vigour. Results showed significant variation occurred in all the characters, and only seed weight displayed a clinal pattern (Melzack and Watts 1982).

In an extensive investigation on correlation of seed characters and geographic coordinates of seed source on Norway spruce, Fober and Giertych (1971) found that elevation and latitude were inversely correlated with seed size and cone shape (diameter and length), and seed weight, respectively. Likewise, seed size of black cherry (Prunus serotina Ehrh.) increased with altitude in Eastern Tennessee (Farmer and Barnett 1972). Calvert (1978) confirmed that white spruce cone length was uniform on any tree sampled in 14 stands, but differed at random depending

on the geographic location of the stand. Seed weight of California red fir (Abies magnifica A. Murr.) was found to be significantly less in the northern part of its range than in the southern part (Franklin and Greathouse 1968). The more stressful weather conditions at higher elevations and latitudes were possibly responsible for the smaller seeds as well as shorter cones. When plus trees were selected for the study of cone and seed characters of Pinus koraiensis, significant differences in cone and seed characteristics were found among them (Han et al. 1982).

Ager and Stettler (1983) confirmed that variation in seed morphology among populations from two soil types of ponderosa pine growing in south Oregon was significant in regard to seed shape and color. Except for seed weight, no significant differences were found between lots within soils.

Sorensen and Miles (1978) studied the relationships of cone and seed weight traits of 89 trees in 9 stands of Douglas fir. Differences among regions for all cone traits, and regression coefficients for changes in cone and seed weights with distance from the ocean, were significant. Cone size and weight decreased, seed weight increased, and the regression coefficient of seed weight on cone weight, based on trees within the regions, increased with the distance from the ocean. For Cupressus, seed weight and cone weight increased from south to north in the Arizonica group (Cupressus arizonica var arizonica, var

nevadensis, var glabra, and var stephensonii) and decreased from south to north in the California Cupressus group (C. goveniana, C. bakeri, C. macrocarpa, C. guadalupensis, C. macnabiana, C. sargentii) (Goggans and Posey 1968).

Another reason for seed quality variation among trees within a species was year of collection. Year effects and interactions of year with other factors accounted for 25 percent of the variation in cotyledon number and 45 percent of the variation in seed weight of Abies procera Rehd. (Sorensen and Franklin 1977). Pulliainen and Lajunen (1984) found that seed yields, seed weight, and other qualities, such as seed composition, varied considerably from year to year in Norway spruce and Scots pine (Pinus sylvestris L.).

When Bingham and Rehfeldt (1970) studied cone and seed yields of 30 to 50 year-old western white pines for eighteen years, they reached the following conclusion: annual cone production was highly variable, but geographic localities and individual trees varied greatly in productivity within a given year. There was a direct relationship between the proportion of filled seed and the size of the cone crop, hence seed collection should be done in high-yielding localities to maximize seed procurement with minimum efforts.

Pitcher (1984) found that black cherry seed weight, size, and endocarp weight varied clinally; those from farther north were larger in all respects. Measurements of

fruit characteristics of red maple (Acer rubrum L.) showed similar significant differences among geographic sources (Townsend 1972). The length of the samara was significantly correlated with latitude but not longitude; length decreased from south to north. Samara characteristics such as width, fruit weight, seed length, and the ratio of width to length, were not significantly correlated with latitude or longitude of source. A study of Castanea sativa Mill. showed that most of the variability of all eight fruit traits appeared to be due to within tree differences and year of collection (Borghetti et al. 1986). In contrast, seed source accounted for little of the total variation of seed traits in chestnut and average seed weight of black walnut (Juglans nigra L.) (Bey 1963). Limstrom (1959) observed that yellow-poplar (Liriodendron tulipifera L.) seed quality varied by tree, stand, and year of collection. Ryynanen (1982) reported that variation in seed quality of Scots pine was considerable only between trees during bad seed years.

Larger black spruce cones tended to have more scales capable of producing seed, and cone length accounted for 70 percent of the variation in seed yield (Haavisto et al. 1988). These findings agree with the work done by Goggans and Posey (1968) on Cupressus and Dickmann and Kozlowski (1971) on Pinus resinosa L. Larger Cupressus cones normally possessed the largest seeds, had more scales, and contained a higher percentage of filled seed. Red pine

cone volume was positively correlated with number of full seeds per cone, total dry weight of seeds per cone, and number of scales per cone. The heaviest cones were generally borne in the middle of the crown and on second-order branches. Seed yield of lodgepole pine (Pinus contorta Dougl.) varied greatly with cone size, parent trees, stands, geographic source, as well as seed extraction methods (Baumgartner et al. 1984).

For yellow birch, long catkins contained more seeds than short ones (Clausen 1980). Variation in white ash (Fraxinus americana L.) seed and wing length appeared to be clinal, while ploidy variation accounted for most of the difference in fruit length, seed width, seedling height, and date of leaf fall. Among-stand variation was significant for all seed traits, nursery traits, seedling survival and height after 3 years in the plantation. Little within-stand variation of the traits was found (Clausen et al. 1981). Seed yield in 8- and 9-year-old yellow birch varied among families and years, and seed quality was poor due to insufficient pollination and differences in flowering phenology (Clausen 1980).

Early collection may also result in poor cone yields, reduced seed weight, and poor germination. Best Douglas-fir seed yields were from fully ripened cones having a high number of seeds per cone (Olson and Silen 1975).

Significant differences have been found in embryo development between stands, between trees within stands,

and between cones within trees. Lower elevations produced longer embryo length and relatively longer cotyledons than higher elevation in white spruce (Zasada 1988). Altitude and latitude of seed source caused variation in the germination rate of lodgepole pine, which is mainly due to incomplete development of embryo and endosperm (Hagner 1980). This is because embryo development depends on both temperature and time (Sarvas 1962).

Damage from insects and diseases has been common for Abies spp. (Edwards 1982). Insect infestation of both cone and seed, prevalent in balsam and Fraser firs (Speers 1974), damages seed quality and seed yields. Cones from Fraser fir trees infested by balsam woolly aphid were found to be shorter and uniformly smaller and lighter than those from uninfested trees (Fedde 1973). Similar influences were not found for balsam fir. McPherson et al. (1982) reported that about 18 percent of black spruce and 45 percent of white spruce seeds were lost to insect and fungi in a good cone year (1980). Similarly, rust (Chrysomyxa pirolata Wint.) significantly reduced seed yield, seed weight, and germination of inland spruce (Sutherland 1981).

Effects of pollution and forest decline. In a study of declining Norway spruce, Stutz et al. (1987) found that seeds and cones from spruce trees with heavy and light needle loss were similar in yield, germination capacity, and temperature response.

The increasing levels of pollution in the atmosphere over the years may have influenced cone and seed production and quality of forest species. Mamejev and Shkarest (1972) found reduction of average seed weight, percent filled seed, and seed germination capacity of eastern white and red pine growing in polluted sites.

Reduced cone production of Norway spruce in highly polluted forests in East Germany was reported by Piesnack (1985). The size of cones and weights of seed of fir from highly polluted areas were significantly reduced (Pelz 1963, cited by Houston and Dochinger 1977). Similar results were also found by Houston and Dochinger (1977) in red pine growing in a polluted site, as reduced seed weight, percent of filled seed, and seed germination capacity. These effects were not observed in white cedar, however, even if the crowns were directly exposed to the source of pollution (nitrate oxide and other pollutants) (Anastasijevic 1982). The effect of SO_2 alone and in combination with fluorine on quality of seeds and cones of Scots pine was studied by Roques et al. (1980, from Bonte 1982). They found that when SO_2 was applied alone, cone weight, cone size, growth development of cone, number of seeds per cone, and percent empty seeds were similar to those of controls from unpolluted sites. When fluorine level was increased and SO_2 level remained the same, the differences were significant. These differences were even

greater when the flourine concentration was the same and the SO_2 concentration was raised.

B. Flowering and Pollination

Timing of pollen release and female receptivity is critical to seed setting. O'Reilly et al. (1982), however, reported that differences in the timing of pollen release and female receptivity among black spruce clones was minor, and that the most important factor was the numbers of male strobili produced by each clone. In white spruce, Ho (1984) found that optimal receptivity occurred when seed cones approached the end of receptivity, which coincided with the peak of pollen shedding. Seed cones pollinated at this stage produced the most filled seed.

The effect of self-pollination in white spruce was studied by Fowler and Park (1983). They showed that self-pollination caused a decrease in seed yield, increased frequency of empty seeds, slightly lower germination and reduced survival of seedlings. These effects are caused by embryonic lethal equivalents due to selfing, which is highly variable for individual trees. Similarly, Park and Fowler (1984) found that inbreeding of a natural population of black spruce led to reduction in seed set, and significant differences in seed weight, percent germination, and seedling height. They concluded that the substantial variation was due to additive genetic and maternal effects. Simpson and Powell (1981) reported that

the proportion of young black spruce trees bearing seed-cones and number of cones per tree increased with tree height. Female "flower" production of some Picea spp. may be correlated with rainfall that occurs in a certain month (Murphy and Miller 1979).

While stress generally prevents flowering in perennials, extreme stress may promote flowering, as though a low probability of survival triggers a final burst of reproduction (Bazzaz et al. 1987). Hence, heavy cone or seed crops are a common phenomenon in trees under extreme stress (Rudolf et al. 1974).

According to Farmer (1981) clonal variation in seed production in any single year was most strongly correlated with percentage of fertilized flowers, while year to year differences in production were associated with variation in the degree of flowering. Unfavorable weather conditions during flowering and cone set or wind currents at critical pollination stages is detrimental to good seed yield and quality (Owens et al. 1987).

Chronic pollution was concluded to affect the reproductive organs of eastern white and red pines even if the concentration was lower than that which causes leaf damage (Houston and Dochinger 1977). Acid rain may also affect reproductive processes in northern hardwood forests due to pH influence on pollen germination and pollen tube growth (Van Ryn et al. 1986, Van Ryn et al. 1988). In pear (Pyrus communis L.), seed count of fruit injured by

pollution revealed a close relationship between the percentage deformation and the number of underdeveloped seeds; continuous pollution at 3.8 ug F per m^3 led to total suppression of development in some varieties (Bonte et al. 1980).

Bonte (1982) studied the mechanism of injury to reproductive structures by fluoride (HF). He found that HF causes alteration of organs which basically are different from one species to another, but resulted in one similar effect - absence of seed. His study on pear showed inhibited growth of the ovary, resulting in zero seed growth. Hence, the question of which organ is affected; is it the pistil or is it pollen? Are the defects in fertilization caused by inhibition of pollen germination or of pollen-tube growth in the stigma? Is it direct action of HF on the ovule or embryo, although no fluorine accumulation was found in the different parts of the fruit, unlike leaves, where such elements are found (Bonte 1982)?

Plants are particularly sensitive to HF during flowering (Sulzbach and Pack 1972, Facteau et al. 1973). When pistils were polluted with HF in vivo, pollen tube growth was unaffected, whether pollination took place before or after a pollution episode. This result suggests that pollen is insensitive to pollution and implies an effect on the pistil (Facteau et al. 1973). In another experiment, when pistils of pear were exposed to pollution alone, the result was a significant inhibition of pollen

germination (Sulzbach and Pack 1972). When Pinus montana and Scots pine pollen were treated with 10 ppm SO_2 for 6 days in a dry atmosphere, pollen germination was unaffected, but germination decreased and pollen tubes burst when the pollen was wet during treatment (Dopp 1931, cited by Houston and Dochinger 1977). Acidification of media by 1.4 ppm SO_2 reduced Populus deltoides pollen germination, but seemed to have had no effect on conifer pollen germination. Failure of pollution to affect pollen germination was attributed to germination media contamination, however, as pH of the media decreased after a certain period (Dopp 1931, cited by Houston and Dochinger 1977).

Shkarlet (1972) was able to show that pollution can modify pollen characteristics. When Scots pine trees were exposed to different levels of pollution, pollen from treated trees was significantly smaller than pollen from nonpolluted stands. Tests with Pinus radiata pollen grains confirmed that SO_2 inhibits pollen germination. The opposite effect was obtained, however, when pollen was exposed to fluoride in vivo (Bonte 1982). Similar treatments stimulated pollen germination for cucumber, tomato (Sulzbach and Pack 1972). It seems that small concentrations of HF have a stimulatory effect; at higher concentrations (above 10 ppm HF) reduction of pollen germination and pollen tube growth can occur.

The stimulation and inhibition of pollen germination depend on pollen species as well as on the pollutant and its concentration, the exposure time, the relative humidity during exposure and some other factors (Wolters and Martens 1987).

C. Seed Germination

Seed germination and early seedling growth are stages in the life cycle of plants that are often most sensitive to inhibiting environmental factors (Schier 1987). Ahlgren and Ahlgren (1981) reported that different forest litters affected seed germination and growth of white spruce and balsam fir, and other forest species. They concluded that these differences appeared to reflect natural habitat preferences. However, germination and growth were not the same, indicating some other factors are involved.

Seeds of the same age, but from different locations in the central Great Plains, achieved higher germination than sources closer to the northern and southern peripheries of the eastern red cedar (Juniperus virginiana L.) distribution (Van Haverbeke and Comer 1985). Paper birch (Betula papyrifera Marsh.) seeds collected from different locations responded differently to light and temperature (Bevington 1986). Seeds from northern sites had a wider temperature range of germination than seeds from southern sites. Northern seed sources germinated more rapidly and achieved higher germination percentages than southern ones. Also, northern seedlots had thinner, more translucent

pericarps than their southern counterparts. Variaton in seed characters (rate of germination and seedling vigor) of Taxus baccata L. varried significantly; only seed weight displayed a clinal pattern (Melzack and Watts 1982).

The variability of seed dormancy and germination of white spruce was also noted by Wang (1976). Significant differences were evident between individual trees, years of collection and pretreatment. He also found that these two physiological responses (dormancy and germination) varied greatly when seed years were poor to mediocre, but were consistent and uniform in good seed years. Significant variation was also observed in the germination of seeds collected from individual Douglas-fir (Ching and Ching 1962), and red alder trees (Alnus rubra Bong) (Radwan and DeBell 1981).

One reason for poor germination is fungus contamination during the prechilling and germination processes which take about two months altogether. The fungus usually responsible is Rhizoctonia solani (Heit and Natti 1969). Another study revealed that low germination was obtained for nonstratified seed at a constant 10°C because of mold problems that infect all treatments. Complete inhibition or severe reduction of germination were evident in some of the germination dishes (Blazich and Hinesly 1984).

Both balsam fir and Fraser fir seeds require stratification to obtain maximum germination in the

laboratory. Seed dormancy in these species may vary from one collection to another from the same source (Edwards 1982).

D. Seedling Development

Seedling establishment often occurs in surface mineral horizons that are affected to a greater degree by acid rain than zones lower in the soil profile. Simulated acid rain did not decrease germination of four pine species, but it did stimulate damping-off, leading to the death of all seedlings in the most acidic level (Schier 1987). When soil was sterilized, mortality was controlled but root growth was inhibited by aluminum toxicity at a soil pH of 3.0. Seedling top growth, however, was significantly greater at pH 3.0 than at less acid treatments; this may possibly be due to greater inputs of N and increased availability of mineral nutrients (Schier 1987).

Responses of seedlings to acid rain differ among species. Development of red pine seedlings at cotyledon stage was inhibited by SO_2 at all concentrations (Constantinidou et al. 1976). The adverse effects were proportional to concentration and duration of exposure, which suggest that their exposure to continuous fumigation in the field, even at low dosages, may adversely influence seedling development and regeneration. Similarly, injury and growth reduction were observed in yellow poplar, sweetgum (Liquidambar styraciflua L.), American sycamore

(Platanus occidentalis L.), and black locust (Robinia pseudoacacia L.) seedlings (Neufeld et al. 1985). Chappelka and Chevone (1986) reported that five-week-old white ash (Fraxinus americana L.) exposed to simulated acid rain had 12 percent less root growth at pH 3.0 than at pH 5.0. Lee and Weber (1979), Reich et al. (1986) and MacDonald et al. (1986), however, found no significant acid rain effect on several forest species seedlings such as sugar maple and jack pine. For Douglas-fir and ponderosa pine seedlings, acid rain with pH as low as 2.0 did not adversely affect shoot growth, but seedlings became limp and developed needle necrosis (McColl and Johnson 1983).

Despite the high acid deposition reported in eastern North America (Mohnen 1988, MacKenzie and El-ashry 1988, Hertel 1988), reproductive capacity of red spruce, balsam fir and Fraser fir seems to be unaffected. There is no indication of reproductive failure in Fraser fir from Mt. Rogers and Mt. Mitchell (Feret 1988). Normal stocking levels of red spruce were reported in the Northeast and Southeast. Regeneration has been found at all elevations, with abundance proportional to overstory species composition (National Acid Precipitation Assessment Program 1989). An increase in regeneration density was evident in areas where mortality was extensive enough to create openings in the stand. Surviving regeneration of spruce seem to be currently adequate in the spruce-fir forest ecosystems (Hertel 1988).

MATERIALS AND METHODS

Site Selection

Differences in seed quality of red spruce, balsam fir, and Fraser fir were determined from seed lots collected from individual trees randomly selected in the declining stands of six major sites: Howland, Maine; Mt. Moosilauke, New Hampshire; Whiteface, New York; Mt. Roger/White Top, Virginia; Mt. Mitchell, North Carolina; and Clingman's Dome Great Smoky Mountain National Park, Tennessee. Ten secondary sites were added in succeeding years to increase the scope of seed quality estimates in the spruce-fir forest ecosystem (Table 1).

A total of three hundred and sixty five (365) trees were selected within the sixteen (16) sites (Table 1). Many of these trees were among those selected and characterized by the Spruce-fir Cooperative Genetic Study Group at the University of Vermont. The following parameters were measured on most of the trees, and the data were supplied by University of Vermont Genetic Group:

1. Age (year)
2. Diameter at breast height (d.b.h.) (cm)
3. Height (m)
4. Crown class (dominant, co-dominant, open grown)
5. Crown condition (decline category in 10 percent increments)
6. Basal area growth in last 20 years (mm^2)

7. Radial growth in the last 20 years (mm^2).

Basal area and radial growth values were derived from increment core data.

Cone Collection

All cones were collected separately from each tree by hand, or by clipping branches with pole or hand shears. Cone maturity indices were based on color: brown for Fraser fir (Franklin 1974) and shining brown for red spruce (Safford 1974). Number of cones collected per tree varied depending on the yield per cone. Cones were cut for seed count estimates. Collection was done for three consecutive years (1986 to 1988). Individual tree collections were sacked separately in either plastic mesh with 18 openings per inch (18 x 18) or paper bags and labelled by a simple number code for site and tree number. All cones were kept in well-aerated condition and transported to the Forestry Sciences Laboratory, Starkville, Mississippi, for extraction, cleaning, and testing. Fir cones were after-ripened indoors for about one month before seed extraction. Most fir had already disintegrated when received, while the red spruce cones were still intact when they reached the laboratory.

Table 1. Collection sites of three forest species studied

No.	Name	Year Collected	No. of Trees Sampled	Elevation (m)	Longitude (°W)	Latitude (°N)
		Balsam Fir				
1.	Greenville, ME*	1987	10	<200	60°60'	45°50'
2.	Acadia NP, Bar Harbor, ME*	1987	11	<200	68°12'	44°23'
3.	Musquodoboit Harbor, NS CAN*	1987	12	<200	63°10'	44°45'
4.	Taymouth, N.B., CAN*	1987	12	<200	66°30'	46°15'
5.	Whiteface Mt., NY	1987	9	~1341	73°59'	44°17'
		1988	13	~1200	73°54'	44°22'
6.	Mt. Moosilauke, NH	1988	20	~750	71°48'	44°00'
7.	Lily Bay, ME*	1988	10	~360	69°34'	45°37'
8.	Howland, ME	1988	10	<200	68°44'	45°13'
		Fraser Fir				
9.	Clingman's Dome, TN (GSMP)	1986	19	~1982	83°30'	35°31'
10.	Roan Mt., NC*	1986	17	~1860	82°40'	36°10'
11.	Mt. Rogers NRA, VA	1987	10	~1746	81°38'	36°30'
12.	Canaan VRA, WVA*	1987	10	~200	79°27'	39°07'
13.	Mt. Mitchell, NC	1987	9	~2037	85°16'	35°44'
		Red Spruce				
14.	Clingman's Dome, TN	1986	13	~1829	83°30'	35°35'
15.	Mt. Moosilauke, NH	1986	10	~750	71°48'	44°00'
16.	Roan Mt., NC*	1986	10	~1860	82°40'	36°10'
17.	Mt. Rogers NRA, VA	1986	20	~1746	81°38'	36°41'
18.	Musquodoboit Harbor, NS, CAN*	1987	15	<200	63°10'	44°45'
19.	Canaan Valley RA, WVA*	1987	9	~200	79°27'	39°07'
20.	Jolicure, NB, CAN*	1987	11	<200	65°45'	45°55'
21.	Mt. Mitchell, NC	1987	15	~2037	85°16'	35°44'
22.	Howland, ME	1987	20	<200	68°44'	45°13'
23.	Whitetop, VA	1987	12	~1936	81°38'	36°39'
24.	Great Smoky Mt. Park, TN/NC	1987	9	~1675	83°30'	35°31'
25.	Whiteface Mt., NY	1988	10	~1480	73°09'	44°22'
26.	Lily Bay, ME*	1988	12	~348	69°34'	45°37'
27.	Howland, ME	1988	10	<200	68°44'	45°13'
28.	Bloomfield, VE*	1988	10	~305	71°40'	44°46'
29.	Central Ontario, CAN*	1988	7	~472	78°06'	45°21'

*Secondary research site of Spruce-Fir Research Cooperative Project.

Seed Extraction, Cleaning, and Upgrading

Procedures and facilities used in extraction, cleaning, and upgrading the seed lots are presented in Figure 1.

Sampling and Test Procedures for Physical Seed Characteristics

Cone Length and Diameter

Empty cones of individual red spruce trees were mixed in a 45 cm diameter bucket and then poured on the table. One hundred cones per tree were randomly selected, placed in cheese cloth, and soaked in water overnight. Soaked cones were then divided into 4 samples of 25 cones each. Cone length and diameter were measured to the nearest 0.01 cm with a caliper. Cone size measurements were not possible for balsam and Fraser firs due to loss of cone integrity in drying and transporting.

Seed Yield

The trees sampled within site were the replicates. Seed yield of each replicate (tree) was calculated by counting the total filled seed extracted divided by the total number of cones per tree. Seed yield of firs was not determined due to inability to count the number of disintegrated cones.

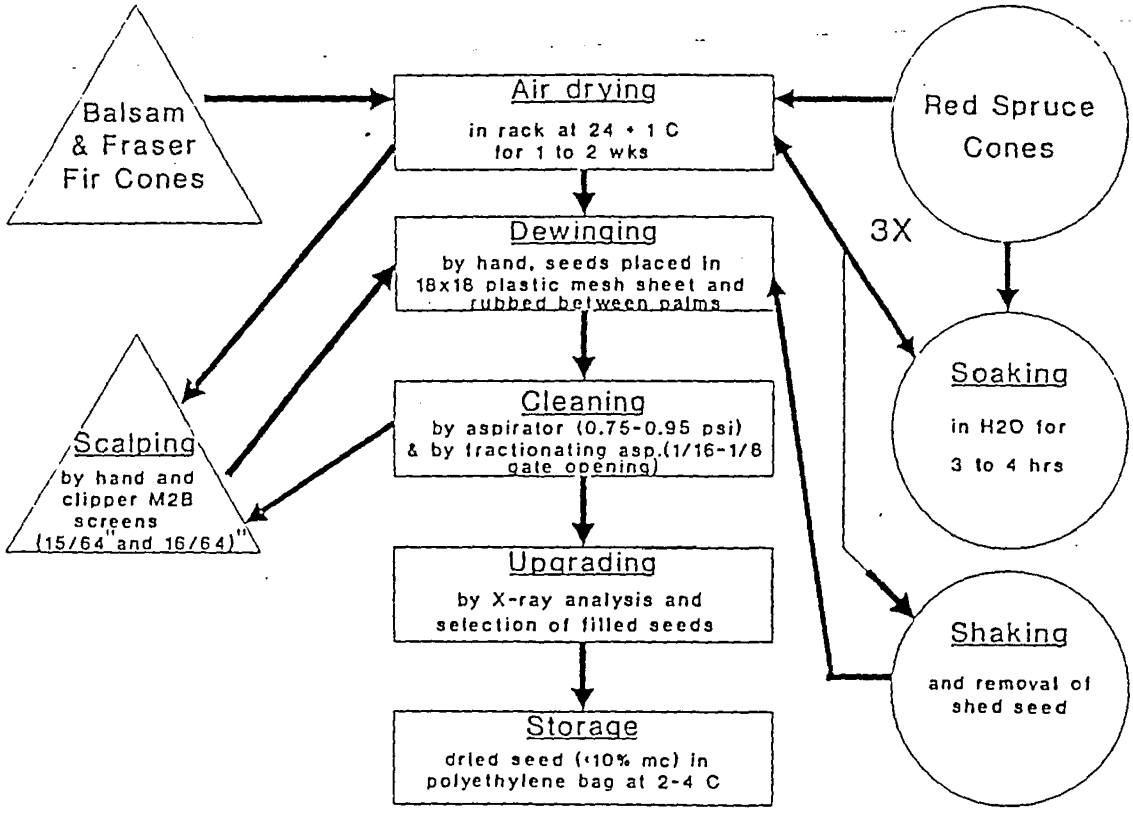

Balsam & Fraser Fir Cones
Air drying
in rack at 24 + 1 C for 1 to 2 wks
Red Spruce Cones
3X
Dewinging
by hand, seeds placed in 18x18 plastic mesh sheet and rubbed between palms
Soaking
in H2O for 3 to 4 hrs
Scalping
by hand and clipper M2B screens (15/64" and 16/64")
Cleaning
by aspirator (0.75-0.95 psi) & by fractionating asp.(1/16-1/8 gate opening)
Upgrading
by X-ray analysis and selection of filled seeds
Shaking
and removal of shed seed
Storage
dried seed (<10% mc) in polyethylene bag at 2-4 C

Figure 1. Flow chart of activities involved in seed extraction and conditioning.

Percentage of Filled and Resin-Filled Seeds

These parameters were assessed in the Fraser fir seed lots only. Resin-filled seed is similar to seed described by Heit (1961). Seeds from each tree were separated into four (4) weight classes in a fractionating aspirator at the Seed Technology Laboratory. The heaviest fraction (spout 1) was designated as best; the second heaviest as good (spout 2); the next heaviest (spout 3) as bad; and, the lightest (spout 4) as the worst. The gate valve of the aspirator was adjusted to accommodate each weight classes. The best and good seed classes were combined, since there was no difference in the ratio of filled and resin-filled seed in both classes based on cutting test. The remaining fractions were discarded. The best and good classes were mixed very well by hand. Two hundred seeds were randomly selected into four samples of 50 seeds each from the mixture per tree. Seeds were cut individually to determine filled and resin-filled conditions as described by Heit and Natti (1969). Tree values were obtained by averaging the four replications.

1000-Seed Weight

Four samples were randomly selected with the number of seed per sample varying according to the size of the seed crop. In 1986, 25 seeds per sample were used for the three species. Sample size was doubled in the succeeding years with the exception of red spruce, which was increased to

100 seeds per sample in 1988. A 1000-seed weight was determined by taking the average of four samples per tree and converting to the weight of 1000 seeds. Weight was calculated to the nearest 0.01 g.

Embryo Length

Cleaned seeds of individual trees were fixed on cardboard with double-sided tape. The cardboard was placed on top of individually packed Kodak AA or M films and exposed in a Faxitron 804 X-ray unit at 3 micro-amperes and 15 to 20 kV for 55 seconds. Exposed films were processed with Kodak X-ray developer and fixer and air-dried. Each radiograph was marked into quadrants and numbered I to IV. Fifteen embryos were measured per quadrant (sample).

A stereomicroscope equipped with a micrometer was used to measure embryo length. A Nicholas Illuminator was placed horizontally below the glass stage plate. A concentrated light beam was directed to the substage condenser lens which deflected the light upward. Embryo cavity, embryo, and other parts of the seeds were visible when light passed through the radiograph. Embryo length was measured to the nearest 0.05 mm.

Seedling Fresh Weight

Four samples of 25 seedlings per tree were randomly selected and carefully removed from the germination blotter at the end of germination tests. Only normal seedlings as

specified in the Association of Official Seed Analysts (AOSA) "Rules for Testing Seeds" (1985) were selected. They were weighed to the nearest 0.001 g with a top loading electronic balance. Remaining gametophytic tissue and seedcoats were removed before seedlings were weighed. Care was exercised to avoid seedling desiccation. Fresh weight per seedling was determined by taking the average of four samples per tree and converting to the weight of one seedling to the nearest 0.01 mg.

Sampling and Test Procedures for Physiological Seed Characteristics

Percent Normal Germination

Seeds sampled for weight and leachate conductivity analyses were used for the laboratory germination test. Seeds of red spruce, balsam, and Fraser fir were soaked in deionized water for 24 hours at 24 $\pm$ 1°C. After leachate conductivity was measured, red spruce seeds were germinated, while balsam and Fraser fir seeds were stratified at 2 to 4°C for 28 days before testing.

Laboratory germination tests were conducted according to AOSA "Rules for Testing Seeds" (1985). Moistened white germination blotters were used with a light-temperature regime of 8 hours light at 30°C and 16 hours dark at 20°C. Trays were rotated daily from top to bottom and front to back. Germination counts were done on alternate weekdays for a period of 21 days. At the end of the testing period,

normal seedlings were randomly selected for seedling fresh weight analysis, and nongerminated seeds were cut and evaluated into three categories as described by AOSA "Rules for Testing Seeds" (1985). Categories of nongerminated seeds were fresh, empty, and dead seed. Abnormal seedlings were also recorded.

Peak Value (PV)

This parameter describes the specific time when rate of germination is highest. It is the maximum quotient derived from all of the cumulative full-seed germination percentages divided by the number of days from sowing (Czabator 1962). Germination test data were used to calculate PV. PV for an individual tree was computed by taking the average PV of the four samples to the nearest 0.01.

Mean Daily Germination (MDG)

This is another measure of germination rate. MDG is the number of seedlings that emerge per day during the entire 21 days of the test. The calculation was done by dividing the total number of normal seedlings that germinated by 21 days, which is the length of germination period. MDG for an individual tree was calculated by taking the average MDG of the four samples.

Germination Value (GV)

This a germination index suggested by Czabator (1962) for tree seeds based on the following formula:

$$GV = PV \times MDG$$

GV for each tree was computed by taking the average GV of four samples.

Leachate Conductivity

In 1986, 25 seeds were used per sample for each tree. In succeeding years, the number of seed per sample per tree was increased to 50 and 100 seeds for the firs and most of the red spruce, respectively. Each sample was placed in a one hundred-cell disposable plastic tray designed for the Automatic Seed Analyser Computer (ASAC-1000), which had been cleaned and filled with deionized water. A flat plexiglass tray cover with several holes was pressed on top of water-filled tray to attain uniformity of water level (4 ml) in every cell. One seed was placed in each cell with forceps. Due to lack of seeds, however, some cells contained water only. Seeds were soaked for 24 hours at-room temperature ($24\pm1°C$). A test clip procedure (Applied Intelligent Systems Inc. 1983) was performed with the ASAC-1000 for correct functioning before conductivity was read with a 4-volt setting. The machine was programmed to rapidly scan and print the desired output one cell at a time. Care was observed that the electrode head was placed in proper position. To avoid contamination between

seed lots, the multi-electrode head was dipped in a blank tray that contained deionized water after every measurement. The blank tray was changed every 2 or 3 hours.

Mean conductivity of leachate per seed was calculated by summing up the conductivity readings of cells that contained seed and dividing by the number of cells. Tree means were based on the average of four samples per tree.

Response to Accelerated Aging

This test was conducted on bulked seed lots. Equal amounts of filled seed from each tree within a research site were combined. Samples were mixed well by hand to avoid damage, especially the fragile fir seeds. Twenty samples of fifty seeds each were randomly withdrawn from the composite lots. Each sample was properly labeled according to the number of days of aging: 0 day, 2, 4, 6, and 7 days, and there were 4 samples per site. For the aging treatment, all samples were placed on top of copper mesh wire inside the air-tight white 15 cm x 15 cm x 5 cm plastic box that contained at least 50 ml distilled water. Each seed lot was secured by a stable divider to avoid seed lot mixture. All boxes were arranged inside the accelerated aging chamber in ascending order, i.e. boxes labelled 7 days were placed at the bottom. This eliminated unnecessary movement of boxes which could cause the seed to be in direct contact with water during sample removal. The

chamber was set at 40± 1°C. Samples were withdrawn on the second, fourth, sixth, and seventh days of the incubation period. Red spruce seeds were directly sown on moistened white blotter and germinated similarly to germination tests as described earlier. The balsam and Fraser fir seeds were soaked overnight before cold stratification as mentioned above. Responses were assessed based on germination percentage.

Response to Temperature Regime

This test was conducted on bulked seed samples only. No test was conducted on balsam and Fraser fir in 1986 due to shortage of seed. In succeeding years, 10 to 25 seeds were placed on each of 25 points on a two-way thermogradient plate (TGP). Each point represented one temperature combination. Plate temperature was set at a maximum of 35°C during the day for 8 hours and a minimum of 10°C at night for 16 hours. Thermistors were installed in nine specific locations in the plate. Each of these thermistors were connected into a temperature scanner where readings can be monitored and recorded daily. The plate was covered with moistened white blotter paper before seeds were placed in each point. Because all of the seeds were small, all seed lots of the same species collected in same year were germinated side by side in the 15 cm x 15 cm area of the TGP. Each area was covered with a separate transparent flexiglass cover. A large common plastic cover

was placed over the entire plate. Substrata were kept moistened during the entire test. Germination counts were done on alternate weekdays for 21 days, and germinated seedlings were removed after counting. Response of seed lots was expressed in cumulative germination.

Statistical Analyses

All analyses were done using SAS procedures (Statistical Analysis System Institute Inc. 1985). Analyses of variance for complete randomized design (CRD) with (Nested data) and without subsampling using General Linear Model were used to test for significance of tree means and site means for seed quality variations. Simple correlations were used to determine the relationships among seed quality variables; between seed quality characters (response variables) and stand conditions as height, diameter, crown class, crown condition, radial growth, and age referred to as independent (or predictor) variables; and between seed quality characters and geographic coordinates of seed sources. Multiple linear regression analysis was used to identify the best model for explaining effects of stand characteristics on seed quality.

RESULTS

Picea rubens Sarg.

A. Physical Characteristics

Cone length and diameter. Trees from the northernmost (latitude 44° to 45° N) and easternmost (longitude 63° to 68° W) populations (Maine, New Hampshire, New York, Canada, and Vermont) produced longer cones (33.5 to 39.3 mm) than southern populations (28.8 to 33.8 mm) (Table 2). Analyses of variance indicated that differences in cone diameter and length among and within populations in 1987 and 1988 were significant at $p=0.05$ (except 1988 cone length). Although cone diameter was statistically different among populations in both 1987 and 1988, real differences were very small ($\leq$0.30 cm)

Seed yield. Seed yield was poor in 1986 but improved markedly in 1987 and 1988 (Table 3). The 1988 crop was best. Seed yields ranged from 7.7 to 18.6 filled seeds per cone as compared to a 1986 range of 1.9 to 4.9. Seed yield was significantly different among and within seed lots or populations ($p=0.01$) in 1986 and 1987. In 1988 however, seed lots differed only at $p=0.05$.

1000-seed weight. Seeds from the southern sites (North Carolina, Tennessee, Virginia and West Virginia) were heavier than seeds produced in northern sites in 1986 and 1987, but there were no differences in weight in 1988 seed lots (Table 4). Highly significant differences

Table 2. Mean diameter and length of red spruce cones, 1987-1988*

Collection site	Diameter (mm)		Length (mm)	
1987				
Musq. Harbor, Nova Scotia	15.9 (0.0)	a	39.3 (0.0)	a
Jolicure, New Brunswick	14.6 (0.0)	b	33.9 (0.1)	b
Howland, Me.	14.2 (0.0)	b	33.5 (0.1)	bcd
Whitetop, Va.	13.8 (0.0)	cd	33.8 (0.1)	bc
Mt. Mitchell, N. C.	13.7 (0.0)	cd	29.7 (0.1)	e
Great Smoky, Mt. Park, Tenn.	13.6 (0.0)	cde	28.8 (0.1)	e
Canaan Valley RA, W. Va.	12.9 (0.0)	e	32.8 (0.1)	bcd
1988				
Howland, Me.	15.3 (0.0)	a	37.7 (0.1)	**
Lily Bay, Me.	14.8 (0.0)	ab	35.4 (0.1)	
Bloomfiled, Vt.	14.3 (0.0)	abc	34.5 (0.1)	
Ontario	14.1 (0.0)	bcd	34.1 (0.1)	
Whitface Mt., N. Y.	13.5 (0.0)	cd	33.4 (0.1)	

* Each mean represents 7-20 sampled trees and 100 measurements per tree (25 cones x 4 subsamples).
Analyses of variances are summarized in Tables 4 and a5 a-b of Appendix. Number in parenthesis is standard error.

** No significant difference at .05 level of probability.
Means followed by same letter in same year and column are not significant at .05 level of probability.

Table 3. Yield of filled seeds per cone of red spruce, 1986-1988*

Collection site	Yield of filled seeds per cone	
1986		
Mt. Rogers, Va.	4.9 (1.3)	a
Mt. Moosilauke, N. H.	3.0 (1.7)	b
Roan Mt., N. C.	1.9 (1.5)	b
Clingman's Dome, Tenn.	2.0 (1.7)	b
1987		
Musq. Harbor, Nova Scotia	24.6 (7.0)	a
Whitetop, Va.	17.0 (7.8)	b
Howland, Me.	12.8 (6.1)	bc
Mt. Mitchell, N. C.	9.6 (7.0)	c
Jolicure, New Brunswick	6.6 (8.2)	d
Canaan Valley RA, W. Va.	4.5 (10.2)	d
Great Smoky Mt. Park, Tenn.	2.0 (9.0)	d
1988		
Howland, Me.	18.6 (4.0)	a
Lily Bay, Me.	16.2 (3.7)	ab
Bloomfield, Vt.	13.7 (4.0)	b
Whiteface, N. Y.	10.3 (4.0)	c
Ontario	7.7 (5.2)	d

* Each yield represents 7-20 sampled trees and 300-1000 cones per tree. Number in parenthesis is standard error
Analyses of variance are summarized in Tables 1-3, of Appendix
Yields followed by same letter in same year and column are not significantly different at .05 level of probability.

Table 4. Mean weight of filled seeds and fresh seedlings of red spruce, 1986-1988*

Collection site	1000-filled seed wt. (g)		fresh wt. per seedling (mg)	
1986				
Mt. Rogers, Va.	4.2	a	15.8	a
	(0.1)		(0.6)	
Roan Mt., N. C.	4.1	a	15.0	a
	(0.2)		(0.8)	
Clingman's Dome, Tenn.	4.0	a	11.1	b
	(0.1)		(0.7)	
Mt. Moosilauke, N. H.	2.8	b	11.1	b
	(0.2)		(0.8)	
1987				
Whitetop, Va.	4.0	a	18.4	ab
	(0.1)		(0.6)	
Canaan Valley RA, W. Va.	3.9	ab	19.0	a
	(0.2)		(0.8)	
Jolicure, New Brunswick	3.5	bc	15.9	cd
	(0.1)		(0.6)	
Mt. Mitchell, N. C.	3.5	bc	16.6	bc
	(0.2)		(0.7)	
Great Smoky Mt. Park, Tenn.	3.3	c	15.5	cde
	(0.2)		(0.7)	
Howland, Me.	3.2	c	15.8	cde
	(0.1)		(0.5)	
Musq. Harbor, Nova Scotia	3.2	c	13.6	f
	(0.1)		(0.6)	
1988 **				
Ontario	3.4		16.9	
	(0.2)		(0.2)	
Lily Bay, Me.	3.3		26.7	
	(0.2)		(0.6)	
Howland, Me.	3.2		16.2	
	(0.2)		(0.7)	
Bloomfield, Vt.	3.0		14.2	
	(0.2)		(0.7)	
Whiteface Mt., N. Y.	3.0		15.8	
	(0.2)		(0.7)	

* Each mean represents 7-20 sampled trees and 4 subsamples per tree.
** No significant difference at .05 level of probability.
Analyses of variance are found in Tables 6-8 of Appendix.
Means followed by same letter in same year and column are not significantly different at .05 level of probability.
Number in parenthesis is standard error.

(p=0.01) among and within populations were observed in 1986 and in 1987. No significant difference was found, however, among 1988 seed lots. There was no indication that primary sites produced lighter seeds than secondary sites in any year.

Embryo length. Embryo length followed the same geographic pattern as seed weight (Table 5). Longer embryos (2.21 to 2.45 mm) were found in southern populations: North Carolina, Tennessee, Virginia, West Virginia; and shorter ones (2.11 to 2.17 mm) were found in Maine, New York, Vermont, and Canada (except Ontario). Highly significant differences (p=0.01) in embryo length were found among and within populations in 1986, 1987, and 1988. Primary sites did not show any pattern of producing longer or shorter embryos than secondary sites.

Seedling fresh weight. The heaviest seedlings came from Lily Bay (26.6 mg) in 1988, Canaan Valley Recreational Area (RA) (19.0 mg) in 1987, and Mt. Rogers (15.8 mg) and Roan Mt. (15.1) in 1986 (Table 4). Seedling weight differences among seed lots were statistically significant (p=0.01) in 1986 and in 1987, but not (p=0.08) in 1988. Differences in the weight of seedlings within each seed lot in 1986, 1987, and 1988 were highly different (p=0.01). Both primary and secondary sites produced comparable seedling fresh weight in all three years.

Table 5. Mean length of embryo of red spruce seeds, 1986-1988*

Collection site	Embryo length (mm)	
1986		
Mt. Rogers, Va.	2.45 (0.03)	a
Roan Mt., N. C.	2.41 (0.04)	a
Clingman's Dome, Tenn.	2.37 (0.03)	a
Mt. Moosilauke, N. H.	1.95 (0.04)	b
1987		
Whitetop, Va.	2.38 (0.04)	a
Mt. Mitchell, N. C.	2.21 (0.04)	b
Canaan Valley RA, W.Va.	2.23 (0.05)	b
Musq. Harbor, Nova Scotia	2.17 (0.03)	b
Jolicure, New Brunswick	2.17 (0.04)	bc
Howland, Me.	2.11 (0.03)	c
1988		
Ontario	2.27 (0.04)	a
Howland, Me.	2.21 (0.04)	a
Lily Bay, Me.	2.10 (0.03)	b
Whiteface Mt., N. Y.	2.09 (0.04)	bc
Bloomfield, Vt.	2.02 (0.04)	bc

* Each mean represents 9-20 sampled trees and 4 subsamples per tree. Analyses of variance are in Tables 9-11 of the Appendix. Means followed by same letter in same year and column are not significantly different at .05 level of probability. Number in parenthesis is standard error.

B. Physiological Characteristics

Percent normal germination. Percent normal germination in three successive years (1986 to 1988) ranged from 62.4 percent to 96.3 percent (Table 6). Poorer germinating seed lots (<80 percent PNG) comprised 75 percent of the 1986 collection, 14 percent in 1987, and none in 1988. Germination was very uniform in 1988; there were no statistical differences among lots. In the earlier two years (1986 and 1987) germination was much more variable. Seed lots from primary sites attained percent normal germination comparable to that of secondary sites in all three years.

Peak value. The low peak values of 1986 seeds suggest lower seed quality in that year than in 1987 and 1988 (Table 6). Peak values among and within populations in both 1986 and 1987 differed significantly ($p=0.01$). In 1988, however, difference among and within seed lots was found to be nonsignificant at $p=0.05$ and highly significantly ($p=0.01$), respectively. Variability of peak value in 1987 (cv=6.90 percent) and 1988 (cv=6.19 percent) seed lots were similar. Peak values of seeds from primary sites were similar to those from secondary sites.

Mean daily germination. Mean daily germination averaged 4.4 (1986) and 4.6 (1987 and 1988) over a 21-day germination period (Table 7). In good seed years (1987 and 1988), the MDG was slightly larger than the poor seed year (1986) (Table 7). The MDG differed significantly

Table 6. Mean red spruce germination and peak value, 1986-1988*

Collection site	PNG		PV	
1986				
Mt. Rogers, Va.	91.7 (3.4)	a	5.6 (0.3)	a
Roan Mt., N. C.	78.5 (4.8)	b	5.1 (0.4)	a
Clingman's Dome, Tenn.	76.8 (4.2)	b	3.8 (0.4)	b
Mt. Moosilauke, N. H.	62.4 (4.8)	c	5.5 (0.4)	a
1987				
Whitetop, Va.	95.9 (1.2)	a	8.0 (0.4)	bcd
Mt. Mitchell, N. C.	94.4 (1.3)	ab	8.4 (0.4)	abc
Jolicure, New Brunswick	93.0 (1.3)	abc	8.4 (0.4)	ab
Musq. Harbor, Nova Scotia	91.6 (1.1)	bc	9.2 (0.4)	a
Canaan Valley RA, W. Va.	91.3 (1.6)	bcd	6.9 (0.5)	def
Howland, Me.	91.3 (1.0)	bcd	7.9 (0.3)	bcde
Great Smoky Mt. Park, Tenn.	79.7 (1.4)	f	5.7 (0.4)	f
1988				
Bloomfield, Vt.	96.3 (2.2)	a	7.1 (0.6)	**
Ontario	94.7 (2.7)	ab	7.6 (0.8)	
Lily Bay, Me.	94.4 (2.1)	ab	8.4 (0.6)	
Howland, Me.	91.0 (2.5)	ab	6.5 (0.7)	
Whiteface Mt., N. Y.	88.3 (2.1)	b	6.6 (0.6)	

* Each mean represents 7-20 sampled trees and 4 subsamples per tree.
** No significant difference at .05 level of probability.
Analyses of variance of PNG and PV are in Tables 15-17 and 18-20 of the Appendix, respectively.
Means followed by same letter in same year and column are not significantly different at .05 level of probability.
Number in parenthesis is standard error.

Table 7. Red spruce mean daily germination and germination value, 1986-1988*

Collection site	MDG (No. of seedlings)		GV	
1986				
Mt. Rogers, Va.	4.4	a	25.0	a
	(0.2)		(1.7)	
Roan Mt., N. C.	3.7	ab	20.0	a
	(0.3)		(2.4)	
Mt. Moosilauke, N. H.	3.7	b	19.8	a
	(0.2)		(2.4)	
Clingman's Dome, Tenn.	3.0	c	12.8	b
	(0.2)		(2.1)	
1987				
Whitetop, Va.	4.6	a	36.8	abcd
	(0.1)		(1.9)	
Mt. Mitchell, N. C.	4.5	ab	37.8	ab
	(0.1)		(2.2)	
Jolicure, New Brunswick	4.4	ab	36.5	abc
	(0.1)		(2.1)	
Howland, Me.	4.4	ab	34.9	bcde
	(0.0)		(1.6)	
Musq. Harbor, Nova Scotia	4.4	ab	40.5	a
	(0.1)		(1.8)	
Canaan Valley RA, W. Va.	4.4	ab	30.4	g
	(0.1)		(2.1)	
Great Smoky Mt. Park, Tenn.	3.8	c	21.9	e
	(0.1)		(2.3)	
1988 **				
Bloomfield, Vt.	4.6		32.4	
	(0.1)		(3.3)	
Lily Bay, Me.	4.5		38.0	
	(0.1)		(3.1)	
Ontario	4.5		34.4	
	(0.1)		(3.9)	
Howland, Me.	4.3		28.8	
	(0.1)		(3.6)	
Whiteface Mt., N. Y.	4.2		28.6	
	(0.1)		(3.3)	

* Each MDG represents 7-20 sampled trees and 4 subsamples per tree.

** No significant difference at .05 level of probability. Analyses of variance of MDG and GV are in Tables 21-23 and 24-26 of the Appendix, respectively.

MDG followed by same letter in same year and column are not significantly different at .05 level of probability.

Number in parenthesis is standard error.

(p=0.01) among seed lots in 1986 and 1987 but not in 1988. There were significant differences (p=0.01) within seed lots each year.

Germination value. Germination values of seed lots in 1986, 1987, and 1988 ranged from 12.8 to 30.0, 21.9 to 40.5, and 28.6 to 3.08, respectively (Table 7). The low germination values in 1986 indicate poor physiological quality of seed lots. Differences among lots collected in 1986, 1987 and 1988 were highly significant in the two earlier years, and nonsignificant in the later year. Within each seed lot, GV was significantly different (p=0.01) each year. Germination values of both primary and secondary sites were similar.

Leachate conductivity. In the poorest seed year (1986), the best seed lot (Mt. Rogers) had the lowest conductivity values (79.9 uA), and the poorest lot (Clingman's Dome), had the highest (90.0 uA). This inverse relationship, however, was not evident in 1987 and 1988 (Table 8). Significant differences (p=0.01) existed among and within seed lots in 1986, 1987, and 1988. Leachate conductivity of seed lots from primary sites was comparable to those from secondary sites.

Response to accelerated aging test. Germination of all seed lots decreased as days of accelerated aging increased (Figure 2 a-c). However, the greatest differences in germination were observed among the 1986 and 1988 seed after four days of aging. Beyond that

Table 8. Mean leachate conductivity of red spruce seed lots, 1986-1988*

Collection site	Leachate conductivity (uA)	
1986		
Clingman's Dome, Tenn.	90.0 (2.0)	a
Mt. Moosilauke, N. H.	86.9 (3.0)	a
Roan Mt., N. C.	86.6 (2.3)	a
Mt. Rogers, Va.	79.9 (1.4)	b
1987		
Musq. Harbor, Nova Scotia	151.3 (2.0)	a
Mt. Mitchell, N. C.	118.2 (2.4)	b
Howland, Me.	110.1 (1.8)	c
Great Smoky Mt. Park, Tenn.	109.6 (2.5)	c
Whitetop, Va.	109.0 (2.1)	c
Canaan Valley RA, W. Va.	108.4 (2.9)	c
Jolicure, New Brunswick	104.38	c
1988		
Howland, Me.	147.1 (1.7)	a
Bloomfield, Vt.	145.3 (1.7)	ab
Lily Bay, Me.	143.7 (1.6)	abc
Ontario	142.7 (2.0)	abc
Whiteface Mt., N. Y.	137.9 (1.7)	d

* Each mean represents 7-20 sampled trees and 4 subsamples per tree.
Analyses of variance are in Tables 27-29 of the Appendix.
Means followed by same letter in same year and column are not significantly different at .05 level of probability.
Number in parenthesis is standard error.

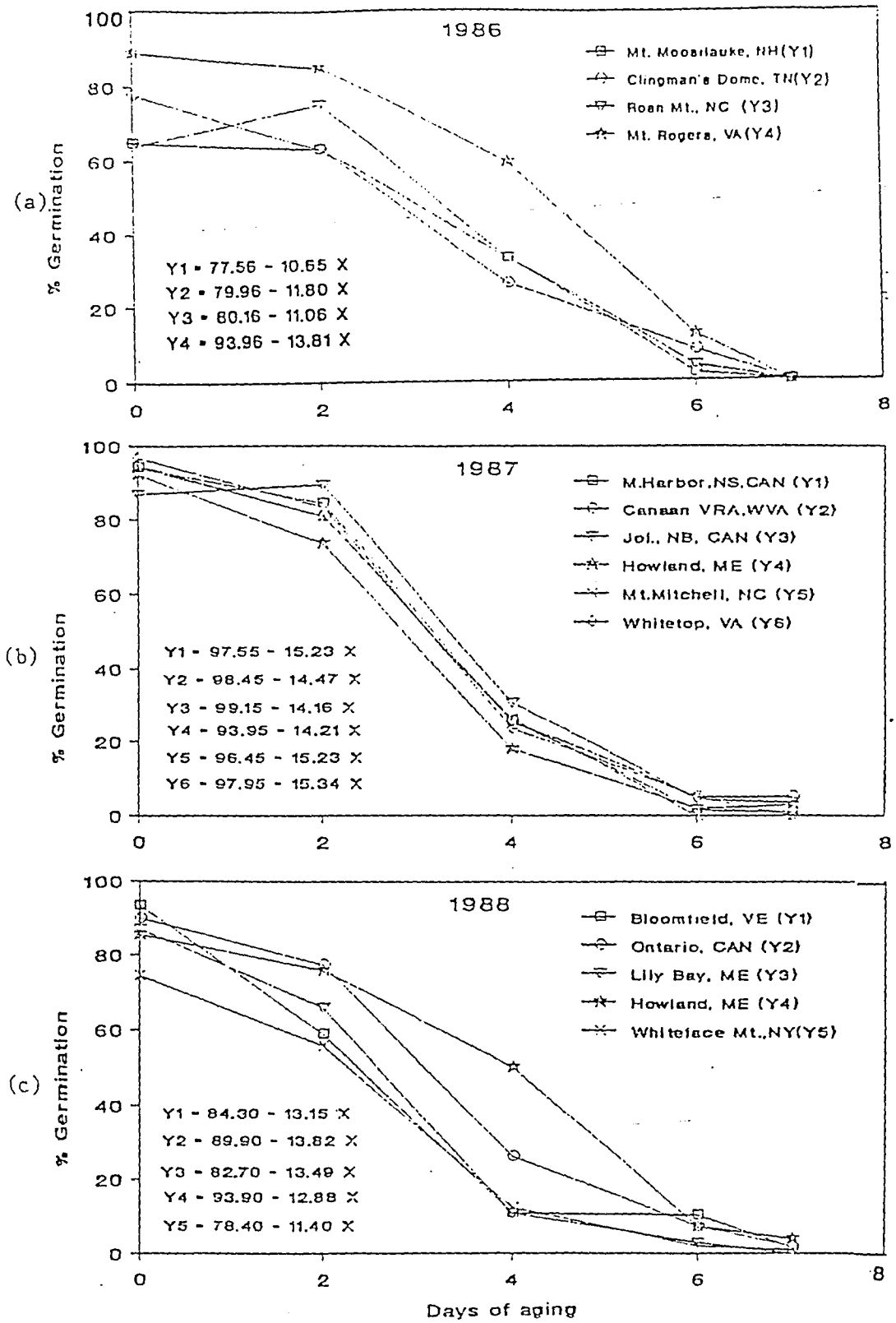


Figure 2 a - c. Germination responses of Picea rubens Sarg. to accelerated aging.

point, germination of all seed lots dropped to equally low levels. The 1987 seed lots showed uniform response after two days of aging (Figure 2 b), indicating a similar vigor condition of all seed lots in that year. At least two seed lots, Roan Mt. (1986) and Jolicure (1987) showed an increase in germination on the second day (Figure 2 a and b). A homogeneity test for regression coefficients showed that no significant difference ($p=0.05$) was found among seed lots in the same collection year, and this was true in all three years. There was no apparent difference between seed lots from primary sites and lots from secondary sites.

Response to germination temperature. Germination occurred at temperatures ranging from 9°-38° C at either constant or alternating cycles of 8 (day) and 16 (night) hours (Figures 3 and 4), with the exception of constant 9° C and constant 38° C.

Individual seed lots responded differently to different temperature gradients. Examples are Musquodoboit Harbor(secondary site) and Howland (primary site) of Figure 3 and Lily Bay (secondary site) and Howland of Figure 4, which were stimulated by warm night temperatures (24°-32° C) and low day temperatures, but inhibited by colder night and day temperatures. The latter conditions favored Mt. Mitchell, Mt. Rogers, and Whitetop Mt. seed lots from primary sites (1987); and Bloomfield, Ontario and Whiteface seed lots in 1988.

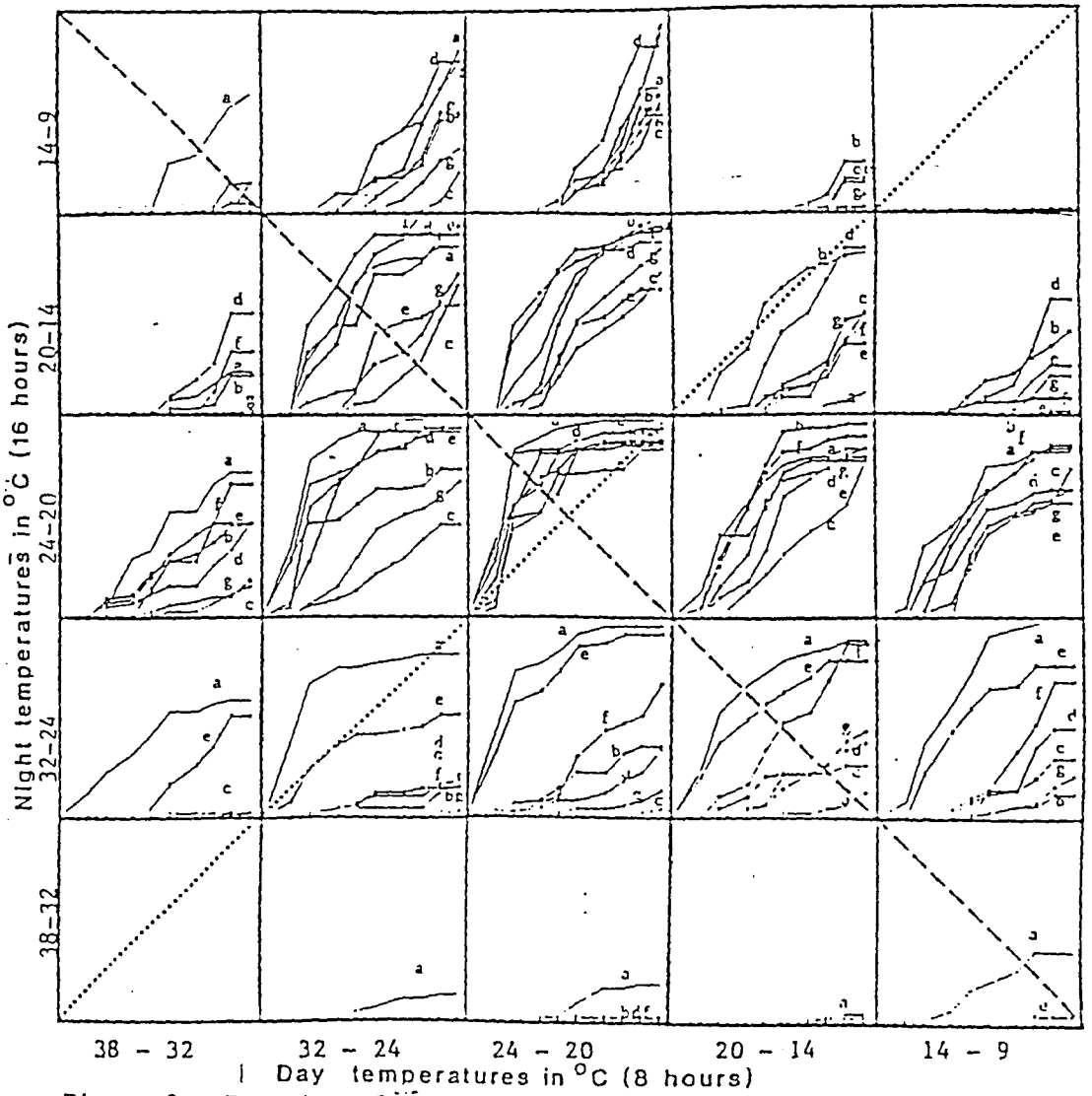


Figure 3. Top view of a two-way thermogradient table showing germination responses of Picea rubens Sarg. seed lots collected in 1987. Each cell represents temperature regime. Germination count was done in 2-day intervals (X-axis) with 10 percent total germination intervals (Y-axis).

Legend: (a) Musquodoboit Harbor; (b) Jolicure, New Brunswick; (c) Canaan Valley RA; (d) Mt. Mitchell; (e) Howland; (...) Constant temp.; (---) Alternating temp.

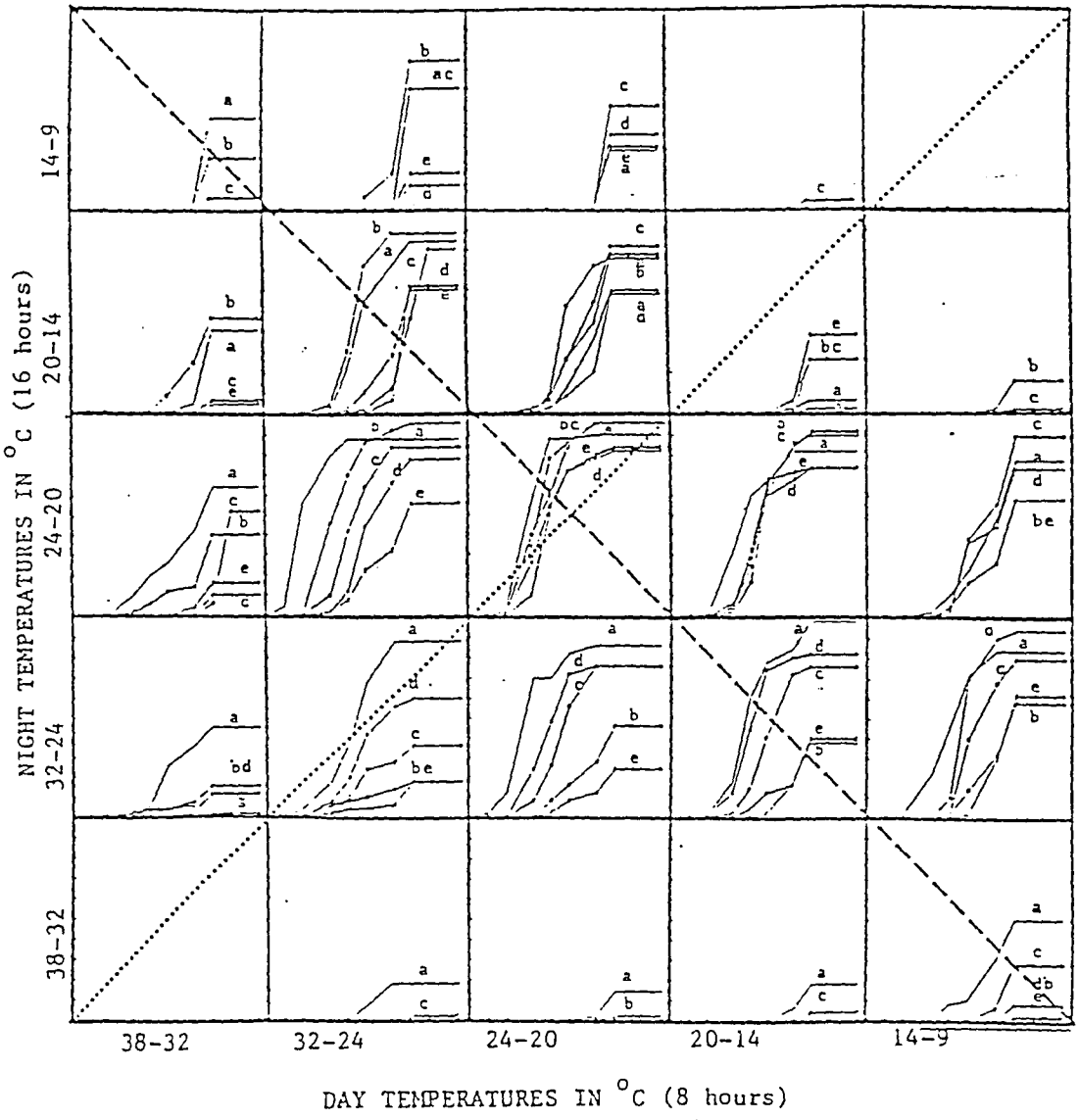


Figure 4. Top view of a two-way Thermogradient table showing germination responses of Picea rubens Sarg. seed lots collected in 1988. Each cell represents temperature regime. Germination count was done in 2-day intervals (X-axis) at 10 percent total germination intervals (Y-axis). Legend: (a) Lily Bay; (b) Bloomfield; (c) Ontario; (d) Howland; (e) Whiteface Mt.; (...) constant temperature; (---) alternating temperature.

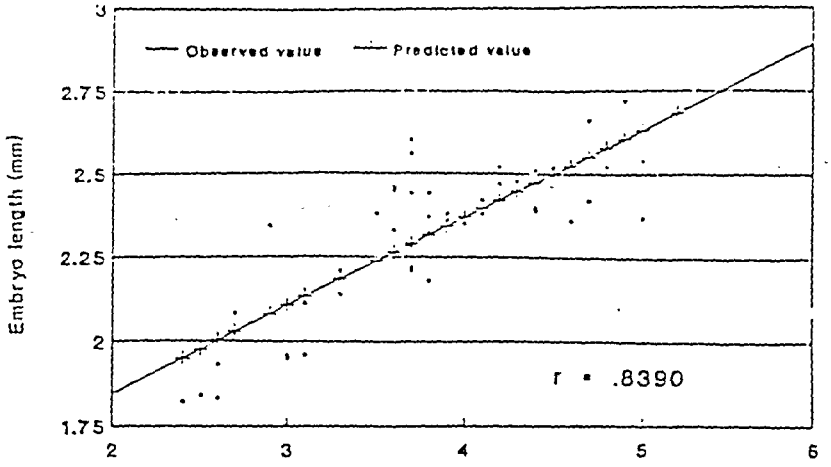
Lily Bay (1988) and Musquodoboit Harbor (1987) seed lots (both secondary sites) were most tolerant of warmer temperature regimes (Figure 3).

Constant temperatures within the range of 20°-24° C proved to be the optimum for most rapid and highest germination percent of seed lots from both primary and secondary sites (Figures 3 and 4). There was no evident pattern of germination behavior of seed lots from either sites.

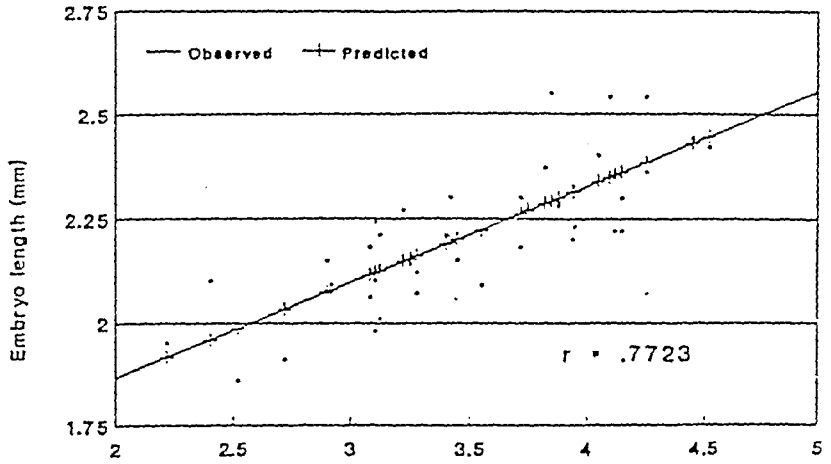
C. Correlations Among Seed Quality Characters

Table 9 summarizes the association among physical seed quality variables and the level of significance obtained from a simple correlation analysis conducted by year. Among the characteristics found to be consistently strongly associated with each other were 1000-seed weight, (Figure 5 a-c) embryo length (Figure 6 a-c), and seedling fresh weight (Figure 7 a-c). Bigger seeds produced bigger seedlings. Other significant associations identified were cone diameter ($r=0.7868$) and cone length ($r=0.7529$) in both 1987 and 1988 collections (no cone size measurement was done in 1986). Cone diameter and length of 1988 seed lots were found to be associated significantly with length of embryo, 1000-seed weight, and fresh weight per seedling. Number of filled seed per cone was strongly associated with embryo length in 1986 collections but not in other years. The same variable was found to be

(a)



(b)



(c)

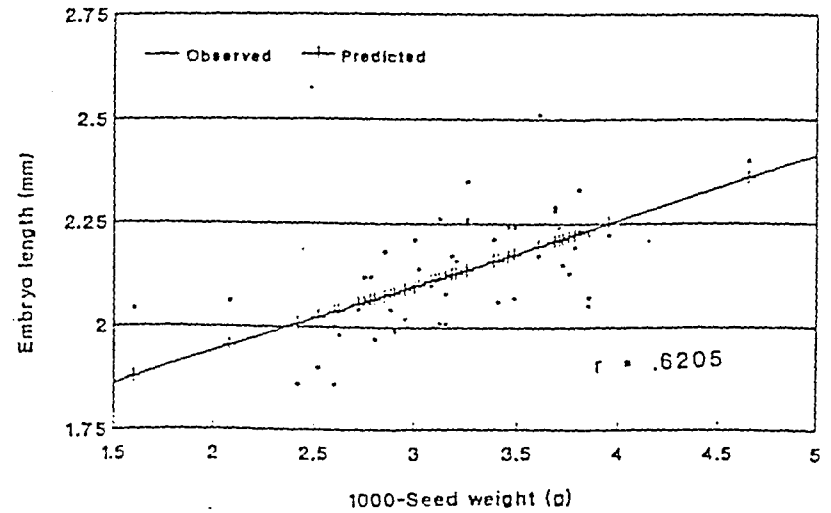


Figure 5 a - c. Relationship between 1000-seed weight and embryo length of Picea rubens Sarg. collected in (a) 1986, (b) 1987, (c) 1988.

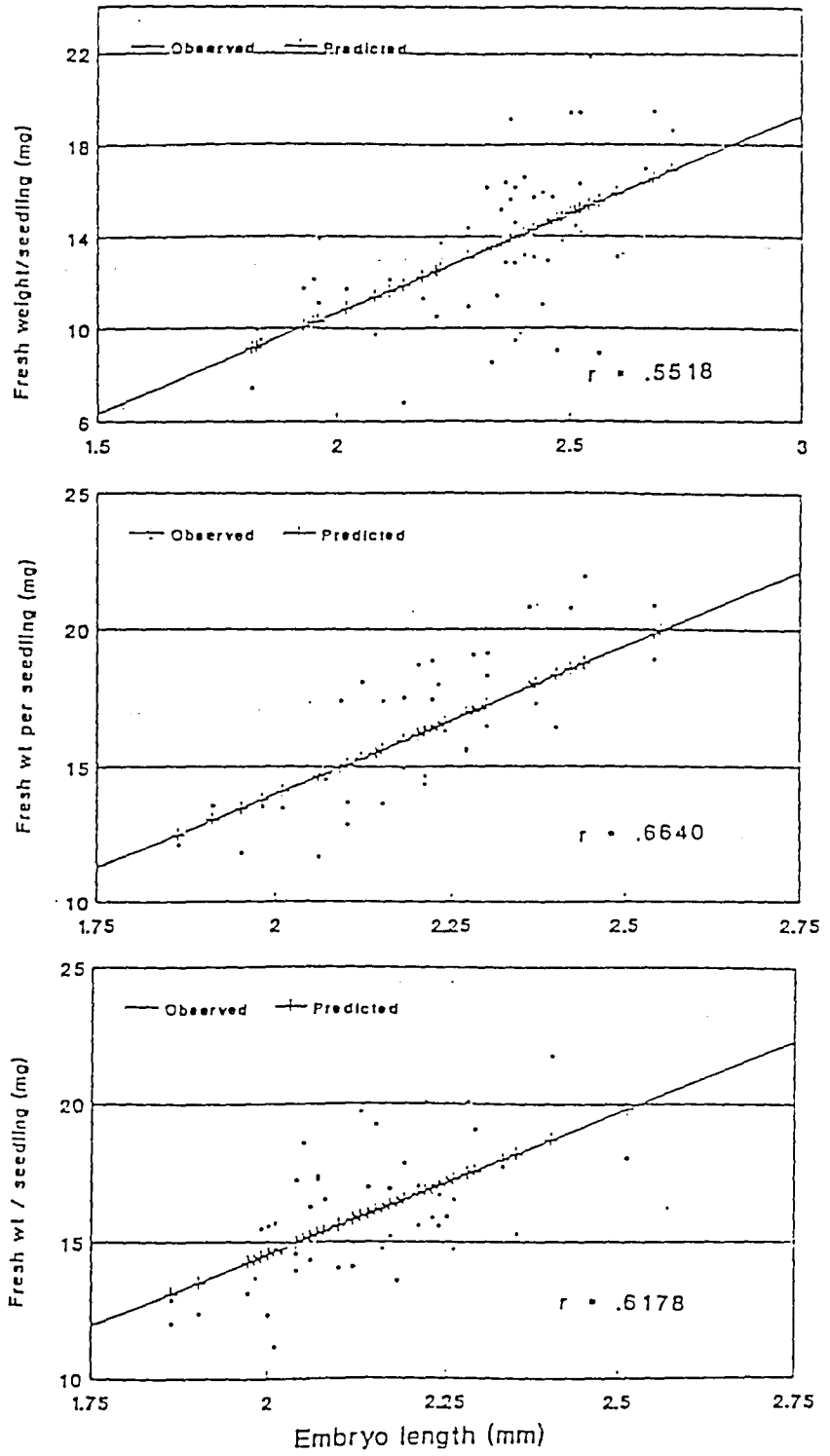


Figure 6 a - c. Relationship between embryo length and seedling fresh weight of Picea rubens Sarg. collected in (a) 1986, (b) 1987, (c) 1988.

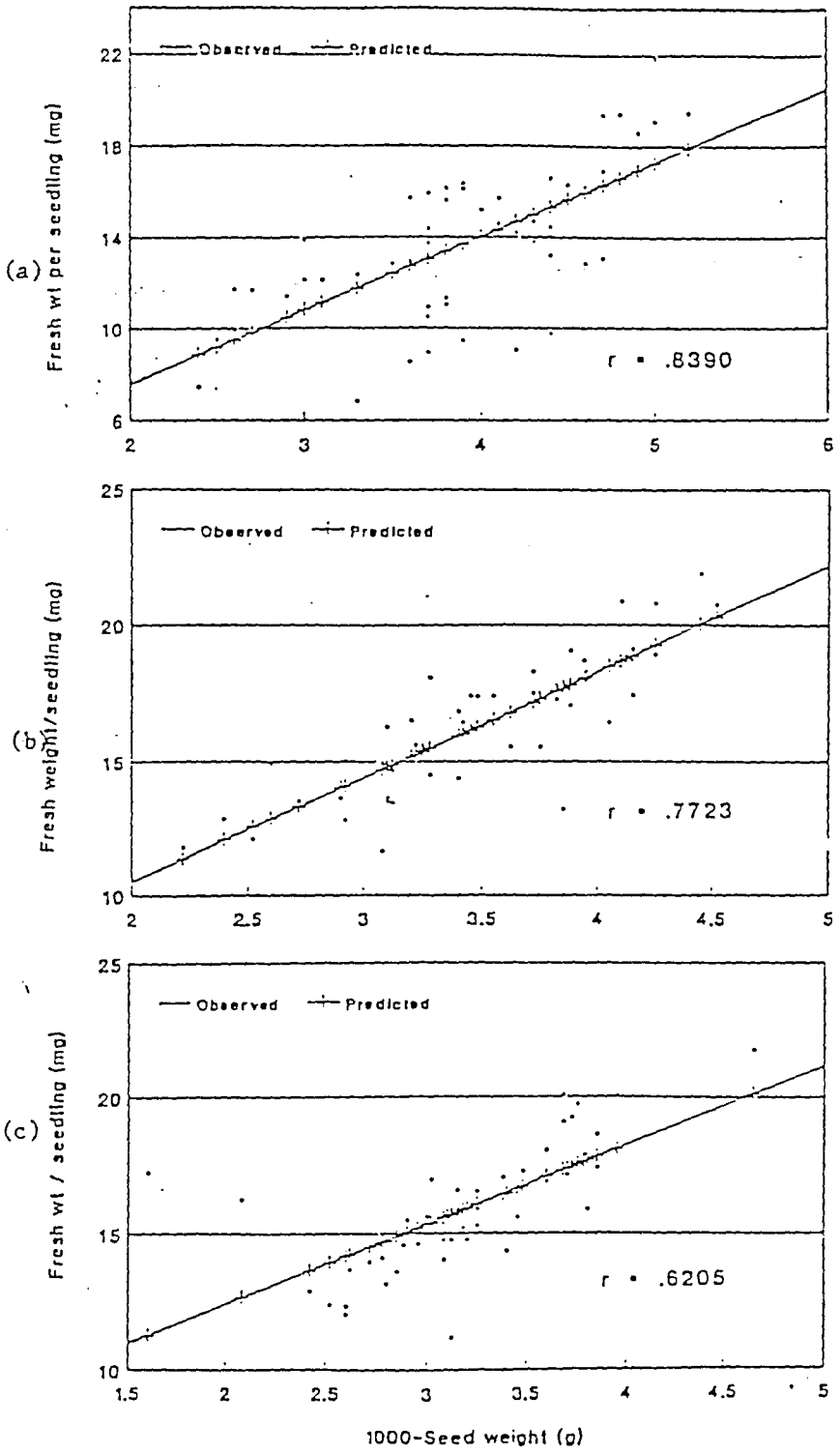


Figure 7 a - c. Relationship between 1000-seed and embryo length of Picea rubens Sarg. collected in (a) 1986, (b) 1987, (c) 1988.

significantly correlated with cone diameter (r=0.5067) and length (r=0.5547) in 1987 (Table 9).

Associations between physical and physiological seed qualities were inconsistent (Table 10). Only 1986 seedling fresh weight and 1987 seed yield were significantly associated with all the physiological seed characteristics (Table 10). A significant negative correlation was observed between seedling fresh weight and leachate conductivity (r=-0.2848) of 1987 seed lots. Seed weight was weakly associated with all physiological characters of seed in three years. Seed lots in 1988 exhibited no significant correlation between physical and physiological seed parameters (Table 10).

The 1987 seed yield, and cone diameter and length parameters were found to be strongly associated with leachate conductivity at p=0.01 (Table 10).

D. Correlations Between Seed Quality and Stand Characteristics

The degree of association between seed quality and stand condition were found to be weak and inconsistent (Table 11). Correlations were strongest in the poorest seed year (1986) . Most of the physiological parameters were negatively correlated with stand conditions, (excluding age) in poor (1986) and better (1987 and 1988 years (Table 11).

Table 10. Correlations between physical and physiological characters of red spruce seed lots.

Physical Characters	% Normal Germination			Peak Value			Germination Value			Mean Daily Germination			Leachate Conductivity		
	1986	1987	1988	1986	1987	1988	1986	1987	1988	1986	1987	1988	1986	1987	1988
No. of filled seed cones	.3904[a/] ** .0042[b/] 52 [c/]	.3177 ** .0003 83	NS	NS	.3867 ** .0003 83	NS	NS	.3977 ** .0002 83	NS	.3906 ** .0042 52	.3188 ** .0033 83	NS	---	.5604 ** .0001 89	NS
Cone length	---	NS	NS	---	NS	NS	---	NS	NS	---	NS	NS	---	.4853 ** .0001 86	NS
Cone diameter	---	NS	NS	---	.2554 ** .0206 82	NS	---	.2382 ** .0312 82	NS	---	NS	NS	---	.5369 ** .0001 87	NS
1000-seed wt.	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	---	NS	NS
Embryo length	NS	.2379 ** .0385 76	NS	NS	NS	NS	NS	NS	NS	NS	.2264 ** .0493 76	NS	---	NS	NS
Fresh wt. per seedling	.6243 ** .0001 53	NS	NS	.5848 ** .0001 53	NS	NS	.6067 ** .0001 53	NS	NS	.6237 ** .0001 53	NS	NS	---	.2848 ** .0062 91	NS

a/ Correlation coefficient (r)
b/ p-value
c/ Number of observations
* Significant at <.05 level of probability
** Highly significant at .01 level of probability
NS Non significant (p=>.05)
--- No data

Table 10. Correlations between physical and physiological characters of red spruce seed lots.

Physical Characters	% Normal Germination			Peak Value			Germination Value			Mean Daily Germination			Leachate Conductivity		
	1986	1987	1988	1986	1987	1988	1986	1987	1988	1986	1987	1988	1986	1987	1988
No. of filled seed cones	** .3904 [a/] .0042 [b/] 52 [c/]	** .3177 .0003 83	NS	NS	** .3867 .0003 83	NS	NS	** .3977 .0002 83	NS	** .3906 .0042 52	** .3188 .0033 83	NS	---	** .5604 .0001 89	NS
Cone length	---	NS	NS	---	** NS	NS	---	** NS	NS	---	NS	NS	---	** .4853 .0001 86	NS
Cone diameter	---	NS	NS	---	** .2554 .0206 82	NS	---	** .2382 .0312 82	NS	---	NS	NS	---	** .5369 .0001 87	NS
1000-seed wt.	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	---	NS	NS
Embryo length	NS	** .2379 .0385 76	NS	NS	NS	NS	NS	NS	NS	NS	** .2264 .0493 76	NS	---	NS	NS
Fresh wt. per seedling	** .6243 .0001 53	NS	NS	** .5848 .0001 53	NS	NS	** .6067 .0001 53	NS	NS	.6237 .0001 53	NS	NS	---	.2848 .0062 91	NS

a/ Correlation coefficient (r)
b/ p-value
c/ Number of observations
* Significant at <.05 level of probability
** Highly significant at .01 level of probability
NS Non significant (p=>.05)
--- No data

Table 10. Correlations between physical and physiological characters of red spruce seed lots.

Physical Characters	% Normal Germination			Peak Value			Germination Value			Mean Daily Germination			Leachate Conductivity		
	1986	1987	1988	1986	1987	1988	1986	1987	1988	1986	1987	1988	1986	1987	1988
No. of filled seed cones	** .3904 [a] .0042 [b] 52 [c]	** .3177 .0003 83	NS	NS	** .3867 .0003 83	NS	NS	** .3977 .0002 83	NS	** .3906 .0042 52	** .3188 .0033 83	NS	---	** .5604 .0001 89	NS
Cone length	---	NS	NS	---	** NS	NS	---	** NS	NS	---	NS	NS	---	** .4853 .0001 86	NS
Cone diameter	---	NS	NS	---	** .2554 .0206 82	NS	---	** .2382 .0312 82	NS	---	NS	NS	---	** .5369 .0001 87	NS
1000-seed wt.	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	---	NS	NS
Embryo length	NS	** .2379 .0385 76	NS	NS	NS	NS	NS	NS	NS	NS	** .2264 .0493 76	NS	---	NS	NS
Fresh wt. per seedling	** .6243 .0001 53	NS	NS	** .5848 .0001 53	NS	NS	** .6067 .0001 53	NS	NS	.6237 .0001 53	NS	NS	---	.2848 .0062 91	NS

[a] Correlation coefficient (r)
[b] p-value
[c] Number of observations
* Significant at <.05 level of probability
** Highly significant at .01 level of probability
NS Non significant (p=>.05)
--- No data

E. Correlations Between Seed Quality and Geographic Coordinates of Seed Source

The degree of association between seed quality and seed source (locations) varied from year to year (Table 12). Among the seed quality variables, only embryo length, 1000-seed weight, seedling fresh weight (1986) and cone diameters (1988) were significantly correlated with all geographic coordinates of seed source (elevation, longitude, and latitude) (Table 12). Embryo length was consistently and significantly correlated with elevation. Latitude was negatively correlated with embryo length ($r=-0.8252$), seed weight ($r=0.7300$) and seedling fresh weight ($r=-0.3736$) in 1986, but not in the better seed years (1987 and 1988). Germination parameters (PNG, PV, GV) were only weakly associated with geographic coordinates (Table 12).

F. Prediction of Seed Quality

There was no "best" equation that consistently and significantly predicted seed quality (Table 13). The predictor variable(s) included in the model that contributed to significant ($p=\leq 0.01$) R^2 were age, basal area, DBH, and crop size.

Table 12. Correlations between red spruce seed quality and stand location.[a/]

Seed Characters	Elevation			Longitude			Latitude		
	1986	1987	1988	1986	1987	1988	1986	1987	1988
Cone diameter	---	NS	-.4403**[b/] .0022[c/] 46[d/]	---	NS	-.3695** .0115 46	---	-.4513** .0001 87	.3716** .0110 46
Cone length	---	NS	-.3041* .0399 46	---	NS	-.2848* .0550 46	---	-.4204** .0001 91	NS
Number of filled seed/cone	NS	NS	-.2845* .0500 48	NS	-.2600** .0139 89	-.4382** .0018 48	NS	-.3556** .0006 89	NS
Embryo length	.8108** .0001 52	.4614** .0001 77	.4469** .0015 48	.8064** .0001 52	-.3883** .0005 77	NS	-.8252** .0001 52	NS	.4469** .0015 48
Seed Weight	.7165** .0001 53	.2873** .0229 91	NS	.7126** .0001 53	NS	NS	.7300** .0001 53	.4107** .0001 91	NS
Seedling Fresh Weight	.3058* .0260 53	.2383* .0229 91	NS	.3251* .0175 53	NS	NS	-.3736** .0059 53	.5182** .0001 91	.3292* .0209 49
Percent normal Germination	NS	NS	-.3090* .0367 46	NS	NS	NS	NS	NS	NS
Leachate Conductivity	---	-.2072* .0488 91	-.4971** .0003 49	---	-.2725** .0090 91	-.2757* .0552 49	---	-.4204** .0001 91	NS
Peak Value	NS	-.2426* .0253 85	NS	NS	NS	NS	NS	-.2621** .0154 85	NS
Germination Value	NS	-.2155* .0476 85	NS	NS	NS	NS	NS	-.2209* .0422 85	NS

a/ Exact locations are in Table 1.
b/ Correlation coefficient (r).
c/ p-value
d/ Number of observations

* Significant at <.05 level of probability
** Highly significant at <.01
NS Non significant (p=>.05)
--- No data

Table 13. Regression equations that predict seed quality of red spruce.*

Characters	Seed Lot	Regression equation model	R^2	Pr > F
Embryo length (Y_1)	1986	$Y_1 = 2.2737 + 0.0016$ (DBH) $- 0.0045$ (Age)	.4080	.0001
	1987	- - - - - - - - - - - - - - - - - - - -	---	---
	1988	- - - - - - - - - - - - - - - - - - - -	---	---
1000-seed wt.(Y_2)	1986	$Y_2 = 3.5277 + 0.0035$ (DBH) $- 0.0123$ (Age)	.3818	.0001
	1987	$Y_2 = 2.8276 + 0.0000$ (Basal)	.3158	.0043
	1988	- - - - - - - - - - - - - - - - - - - -	---	
Number of filled per (Y_3) cone	1986	$Y_3 = 5.6814 - 0.0096$ (Crop size)	.3784	.0001
	1987	$Y_3 = 44.1571 - 0.5027$ (Age)	.3641	.0029
	1988	- - - - - - - - - - - - - - - - - - - -		
Cone diameter (Y_4)	1986	- - - - - - - - - - - -	---	---
	1987	$Y_4 = 1.8744 - 0.0093$ (Age)	.2862	.0103
	1988	- - - - - - - - - - - - - - - - - - - -	---	---
Cone length (Y5)	1986	- - - - - - - - - - - - - - - - - - - -	---	---
	1987	- - - - - - - - - - - - - - - - - - - -	---	---
	1988	- - - - - - - - - - - - - - - - - - - -	---	---
Fresh wt. (Y_6) seedling	1986	$Y_6 = 18.5139 - 0.0533$ (Age) $+ 0.000009$ (Basal)	.1843	.0125
	1987	- - - - - - - - - - - - - - - - - - - -	---	---
	1988	- - - - - - - - - - - - - - - - - - - -	---	---
% Normal (Y_7) germination	1986	$Y_7 = 112.8531 - 0.3125$ (Age) $+ 0.0006$ (Basal)	.2769	.0009
	1987	- - - - - - - - - - - - - - - - - - - -	---	---
	1988	- - - - - - - - - - - - - - - - - - - -	---	---
Peak value (Y_8)	1986	$Y_8 = 6.1551 - 0.00004$ (Basal)	.2073	.0015
	1987	$Y_8 = 12.2532 - 0.0730$ (Age)	.3421	.0027
	1988	- - - - - - - - - - - - - - - - - - - -	---	---
Germination (Y_9) value	1986	$Y_9 = 35.0407 - 0.1193$ (Age) $- 0.0003$ (Basal)	.2852	.0007
	1987	$Y_9 = 55.5508 - 0.3544$ (Age)	.3239	.0037
	1988	- - - - - - - - - - - - - - - - - - - -	---	---
Leachate (Y_{10}) conductivity	1986	- - - - - - - - - - - -	---	---
	1987	$Y_{10} = 188.5684 + 1.8765$ (Age)	.4857	.0002
	1988	- - - - - - - - - - - - - - - - - - - -	---	---

Y_n Seed quality characters

* Regression model with significant R^2 at .01 level of probability is shown.

--- R^2 obtained was non significant therefore equation is not shown ($p>.05$).

Abies balsamea (L.) Mill.

A. Physical Characteristics

1000-seed weight. Seed weight ranged from 7.8 to 9.7 g in 1987 and 6.9 to 9.7 g in 1988 (Table 14). Both heaviest and lightest seed lots in 1987 came from Maine. In 1988, Lily Bay, also from Maine, was heaviest, and Whiteface Mt. was lightest. Seed lots differed among and within seed lots in both 1987 and 1988. The coefficient of variation was two times higher (3.87 percent) in 1987 than in 1988 (1.76 percent).

Embryo length. Differences in embryo length were very small (Table 14). Embryo length did not differ among seed lots in 1987 ($p=0.05$), but, it differed significantly in 1988 ($p=0.01$). Variations in embryo length in 1987 (cv=1.81 percent) and 1988 (cv=1.55 percent) were almost the same.

Seedling fresh weight. Seedlings were heavier (27.3 to 33.6 mg) in 1988 than in 1987 (23.2 to 30.0 mg) (Table 14). There was little weight difference (0.70 mg), however, between seedlings grown from collections on Whiteface Mt. in two different years. Seedling weight differed significantly within seed lots both years.

B. Physiological Characteristics

Percent normal germination. There were no significant differences in PNG in 1987, and only slight

Table 14. Embryo length, seed and seedling fresh weight of balsam fir, 1987-1988*

Collection site	Embryo Length (mm)		Seed Weight (g)		Fresh wt/ seedling (mg)	
1987**						
Bar Harbor, Me.	4.0**		9.7	a	27.2	ab
	(0.1)		(0.5)		(1.9)	
Nova Scotia	4.0		8.9	abc	23.2	b
	(0.9)		(0.4)		(1.6)	
New Brunswick	3.9		9.4	ab	24.9	b
	(0.1)		(0.5)		(1.6)	
Whiteface Mt., N. Y.	3.8		9.4	ab	30.0	a
	(0.1)		(0.5)		(1.9)	
Greenville, Me.	3.7		7.8	c	23.5	b
	(0.1)		(0.5)		(1.9)	
1988						
Lily Bay, Me.	4.0	a	9.7	a	33.6	a
	(0.1)		(0.5)		(1.4)	
Mt. Moosilauke, N. H.	4.0	a	8.5	b	31.3	ab
	(0.1)		(0.3)		(1.0)	
Whiteface, N. Y.	3.7	b	6.9	c	29.3	bc
	(0.1)		(0.4)		(1.2)	
Howland, Me.	3.6	b	8.9	ab	27.5	c
	(0.1)		(0.5)		(1.4)	

* Each mean represents 7-20 sampled trees and 4 subsamples per tree.
Analyses of variance of embryo length, seed wt, and seedling wt are in Tables 30-31, 32-33, and 34-35, respectively.

** No significant difference at .05 level of probability.
Means followed by same letter in same year and column are not significantly different at .05 level of probability.
Number in parenthesis is standard error.

differences (p=0.05) in 1988 (Table 15). No lot had a PNG above 75 percent, but 1988 seeds germinated somewhat better than those of 1987.

Peak value. Seeds from Whiteface Mt., New York were the most vigorous among 1987 (3.2) and 1988 (5.3) collections (Table 15). The lower peak values in 1987 (2.0 to 3.2) compared to 1988 (3.7 to 5.3) indicated poorer seed quality in 1987 seed lots. There were significant differences (p=0.05) among the 1988 lots, but not among 1987 lots.

Mean daily germination. Seed lots in 1987 had lower MDG (1.8 to 2.7 seedlings) than 1988 (2.9 to 3.5 seedlings) (Table 15). Direct comparison of lots from Whiteface Mt. collected in 1987 and 1988 showed only a small difference (0.5) in MDG. Seed lots from Canada (New Brunswick and Nova Scotia) had the lowest MDG values in both years. Differences among lots were significant in 1988 (p=0.05), but not in 1987. Variability of MDG was twice as high (cv=20.99 percent) in 1987 than in 1988 (cv=9.42 percent).

Germination value. Germination values of 1987 lots were lower than those of 1988 (Table 16). The two Canadian seed lots were the most physiologically inferior among the seed lots in 1987 (Table 16). Germination values were found to be significant (p=0.05) and nonsignificant (p=0.09) in 1987 and 1988, respectively.

Table 15. Percent normal germination, peak value, and mean daily germination of balsam fir, 1987-1988*

Collection site	PNG		PV		MDG (No. of seedlings)	
1987**						
Whiteface Mt., N. Y.	56.9		3.2		2.7	
	(7.3)		(0.4)		(0.3)	
Bar Harbor, Me.	46.4		2.7		2.3	
	(5.7)		(0.3)		(0.3)	
Greenville, Me.	40.3		2.6		2.0	
	(6.8)		(0.4)		(0.3)	
New Brunswick	38.0		2.3		1.8	
	(5.5)		(0.3)		(0.3)	
Nova Scotia	34.9		2.0		1.8	
	(5.5)		(0.3)		(0.3)	
1988						
Mt. Moosilauke, N. H.	74.4	a	4.9	ab	3.5	a
	(3.0)		(0.3)		(1.4)	
Howland, Me.	66.8	ab	3.8	bc	3.4	ab
	(3.9)		(0.4)		(2.1)	
Whiteface Mt., N. Y.	71.6	ab	5.3	a	3.2	ab
	(4.0)		(0.4)		(1.9)	
Lily Bay, Me.	60.1	b	3.7	c	2.9	b
	(4.2)		(0.4)		(2.0)	

* Each GV represents 9-20 sampled trees and 4 subsamples per tree.

** Not significant different at p=.05 level.
Analyses of variance of PNG, PV, and MDG are in Tables 36-37, 38-39, and 40-41 of the Appendix, respectively.
Means followed by same letter in same year and column are not significantly different at .05 level of probability.
Number in parenthesis is standard error.

The coefficient of variation in 1987 was 39.56 percent, over twice as much as in 1988 (16.88 percent).

Leachate conductivity. Conductivity readings in 1988 seeds (155.2 to 179.6 μA) were higher than in 1987 seeds (132.3 to 159.5 μA) (Table 16). This result was unexpected, considering that 1987 seed lots were poorer in quality than those of 1988. Conductivity is expected to be higher in the poorer seed lots due to membrane deterioration. Significant differences ($p=0.05$) in leachate conductivity existed among and within seed lots in both 1987 and 1988.

Response to accelerated aging test. Germination response of all seed lots decreased as days of accelerated aging increased (Figure 8 a and b). The greatest differences among seed lots were observed after two days of aging. At this point, the most vigorous seed lots were evident; Greenville, Nova Scotia, and Whiteface Mt. (primary site) were best in 1987; Mt. Moosilauke (primary site) and Lily Bay (secondary site) in 1988. However, germination of all seed lots dropped to zero after 6 days of aging. A homogeneity test for regression coefficients suggested that 1987 seed lots responded significantly different ($p=0.05$) to accelerated aging. No significant difference, however, was found among the 1988 lots.

Response to germination temperature. All seed lots (1987 and 1988) germinated in a wide range of temperature regimes in either constant or alternating mode. The 1987

Table 16. Germination value and leachate conductivity of balsam fir, 1987-1988*

Collection site	GV		Leachate conductivity (uA)	
1987				
Whiteface Mt., N. Y.	10.3 (1.8)	a	137.2 (5.4)	c
Bar Harbor, Me.	6.7 (1.4)	ab	157.8 (4.9)	ab
Greenville, Me.	6.5 (1.7)	ab	151.7 (5.1)	ab
New Brunswick	4.7 (1.4)	b	132.3 (4.7)	c
Nova Scotia	4.0 (1.4)	b	159.5 (4.7)	a
1988**				
Mt. Moosilauke, N.H.	18.1** (1.7)		155.2 (2.)	c
Whiteface Mt., N. Y.	17.7 (3.0)		179.6 (2.5)	a
Howland, Me.	12.8 (2.4)		168.6 (2.9)	b
Lily Bay, Me.	11.7 (2.4)		173.6 (2.9)	ab

* Each mean represents 9-20 sampled trees and 4 subsamples per tree.

** No significant difference at .05 level of probability
Analyses of variance of GV and leachate conductivity are in Tables 42-43 and 44-45 of the Appendix, respectively.

Means followed by same letter in same year and column are not significantly different at .05 level of probability.
Number in parenthesis is standard error

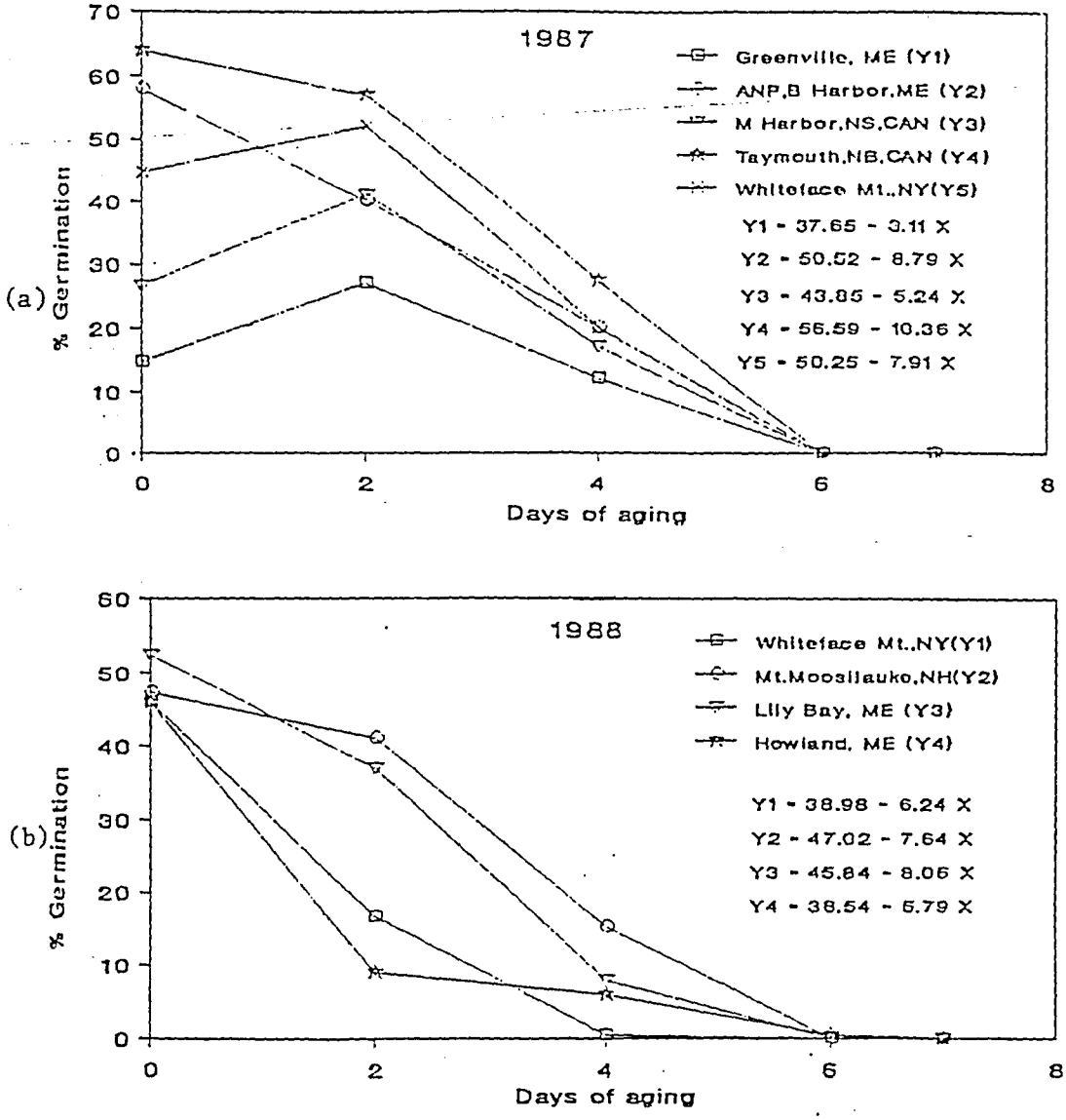


Figure 8 a - b. Germination responses of Abies balsamea (L.) Mill. to accelerated aging.

(Figure 9) lots were found to be more sensitive to high (>32°C) and long (16 hours) warm temperatures with decreasing or increasing day temperatures as compared to 1988 lots (Figure 10).

The highest, most rapid, and most uniform germination responses were found in temperatures ranging from 20°-32°C for 16 hours with decreasing or increasing day temperatures (Figures 9 and 10). The 1988 seed lots (Figure 10) germinated better, faster, and more uniformly than did the 1987 lots (Figure 9).

Seed lots from Whiteface Mt.(primary site) and Bar Harbor (secondary site) in 1987, Lily Bay (secondary site), and Mt. Moosilauke (primary site) 1988 were most tolerant of different temperature levels in both constant and alternating modes. Seeds from Whiteface Mt. (1987), for instance, were stimulated by the long warm temperature (24°-32°C) as day temperature decreases to a level above 9°C. The 1988 lots responded in a wider temperature range than did those of 1987 (Figure 9).

Long (16 hours) warm temperatures (32°-38°C) with decreasing or increasing day (8 hours) temperatures inhibited germination more than long cold (9°-14°C) night temperatures. Surprisingly, all seed lots from primary and secondary sites in both years responded equally well in warm day temperatures (32°-38°C) with decreasing or increasing night temperatures and in cold (9°-14°C) day

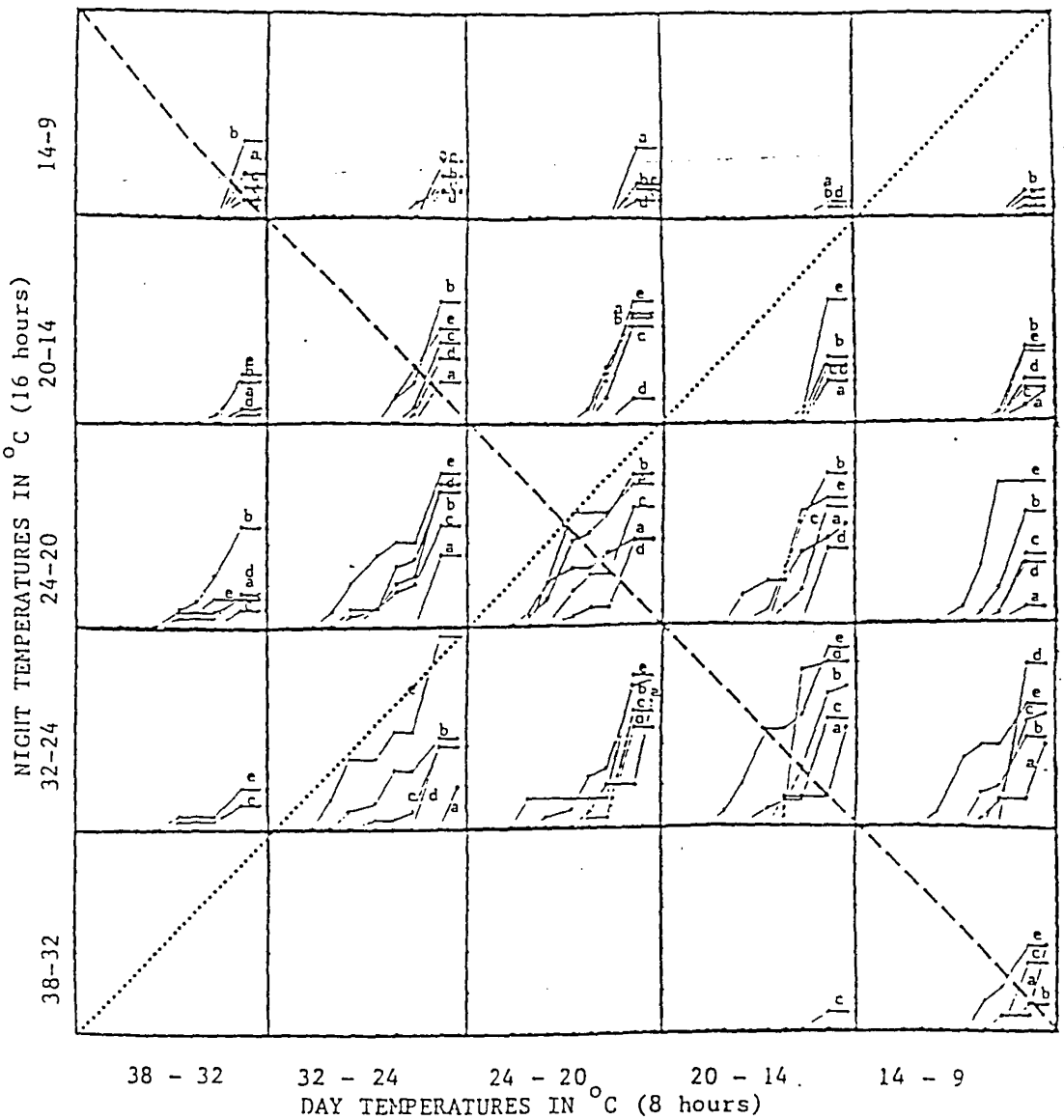


Figure 9. Top view of a two-way thermogradient table showing germination responses of Abies balsamea (L.) Mill. seed lots collected in 1987. Each cell represents temperature regime. Germination count was done in 2-day intervals and 20 percent total germination intervals (Y-axis). Legend: (a) Greenville; (b) Bar Harbor; (c) Nova Scotia; (d) New Brunswick; (e) Whiteface Mt; (....) constant temperature; (---) alternating temperature.

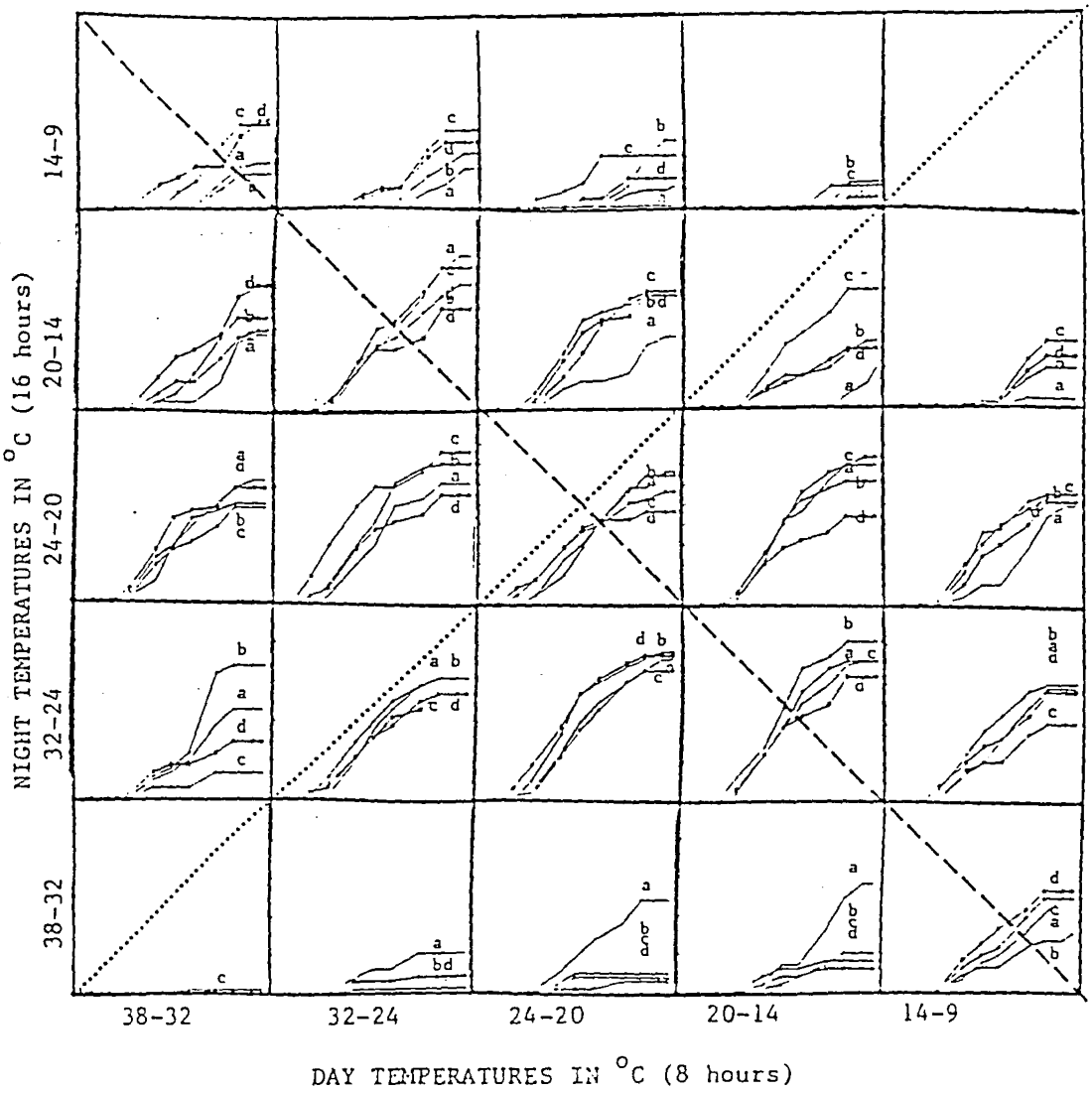


Figure 10. Top view of a two-way thermogradient table showing germination responses of Abies balsamea (L.) Mill. seed lots collected in 1988. Each cell represents temperature regime. Germination count was done in 2-day intervals (X-axis) and 20 percent total germination intervals (Y-axis). Legend: (a) Howland; (b) Lily Bay; (c) Mt. Moosilauke; (d) Whiteface Mt.; (...) constant temperature; (---) alternating temperature.

with increasing or decreasing night temperatures (Figures 9 and 10).

Critical temperatures which inhibited germination completely in all seed lots (primary and secondary sources) were constant cold (9°-14°C) and constant warm (32°-38°C) temperatures. Long warm (32°-38°C) temperatures were more detrimental to 1987 seeds than to 1988 lots.

C. Correlation Among Seed Quality Characters

Embryo length, seed weight and seedling fresh weight characters were strongly and consistently associated with each other (Table 17). Their correlations are graphically presented in Figures 11 a-b (seed weight and embryo length), 12 a-b (seed weight and seedling fresh weight), and 13 a-b (embryo length and seedling fresh weight).

As expected, leachate conductivity was found to have consistent negative correlation with PNG (r=-0.2963 and -0.4140), MDG (r=-0.2807 and -0.4084), 1987 PV (r=-0.2882) and GV (r=-0.2685 and -0.3043) in both years (1987 and 1988) (Table 18).

A strong relationship was indicated between seedling fresh weight and physiological qualities (PNG, PV, GV, and MDG), excluding leachate conductivity in 1987 (Table 19). Peak value showed a significant negative correlation with seed weight in 1988, but not in 1987. Other relationships were all nonsignificant (Table 19).

Table 17. Correlations among physical characters of balsam fir seed lots collected in two years.

	Embryo length		1000-seed wt.	
	1987	1988	1987	1988
Embryo length	—	—		
1000 seed wt.	0.7742** [a/] 0.0001 [b/] 51 [c/]	0.6981** 0.0001 53	—	—
Fresh wt/seedling	0.3080** 0.0332 48	0.6990** 0.0001 53	0.4081** 0.0001 50	0.7431** 0.0001 53

a/ Correlation coefficient (r)
b/ p - value
c/ Number of observations
* Significant at <.05 level of probability
** Highly significant

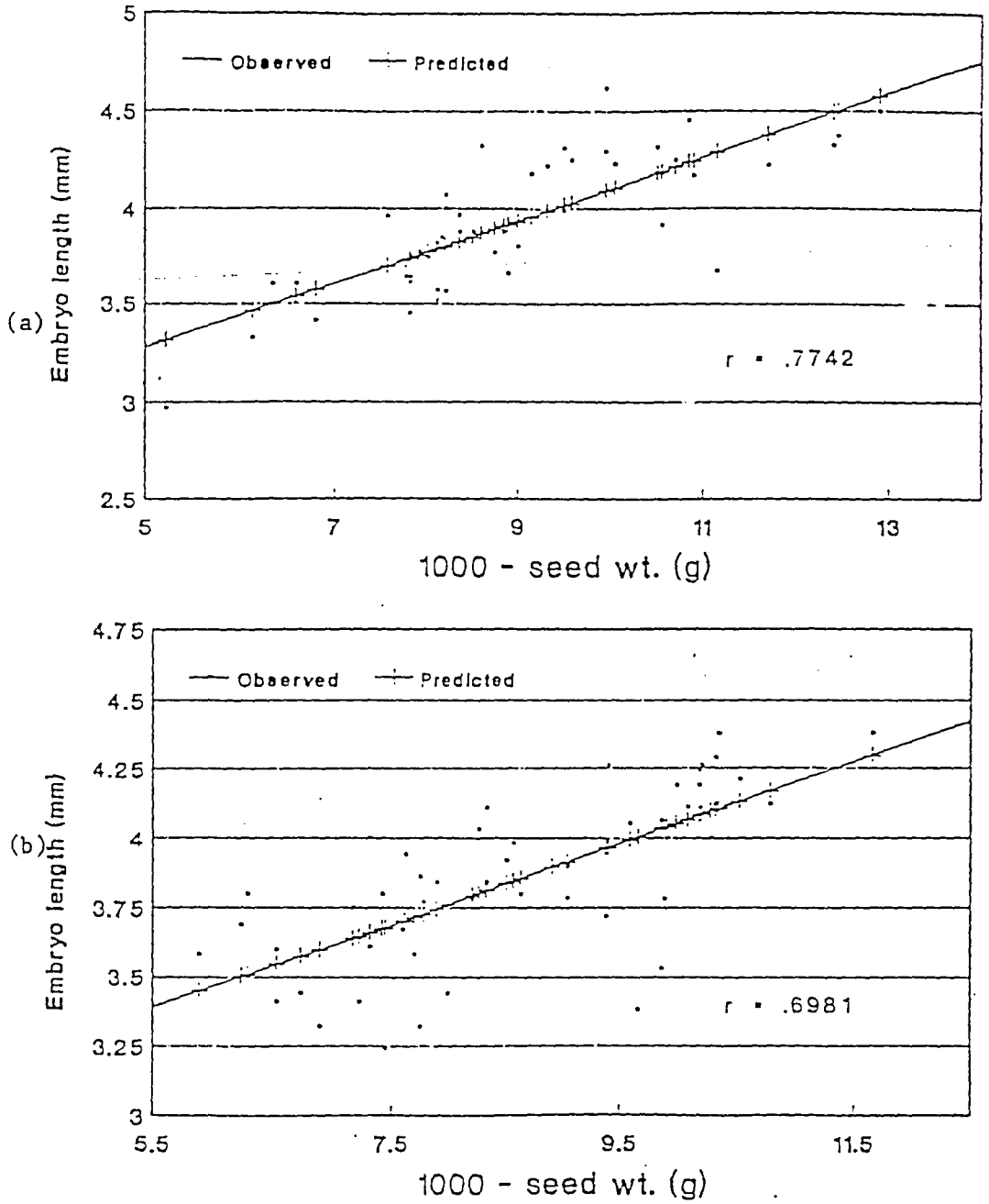


Figure 11 a - b. Relationship between 1000-seed weight and embryo length of Abies balsamea (L.) Mill. collected in (a) 1987 and (b) 1988.

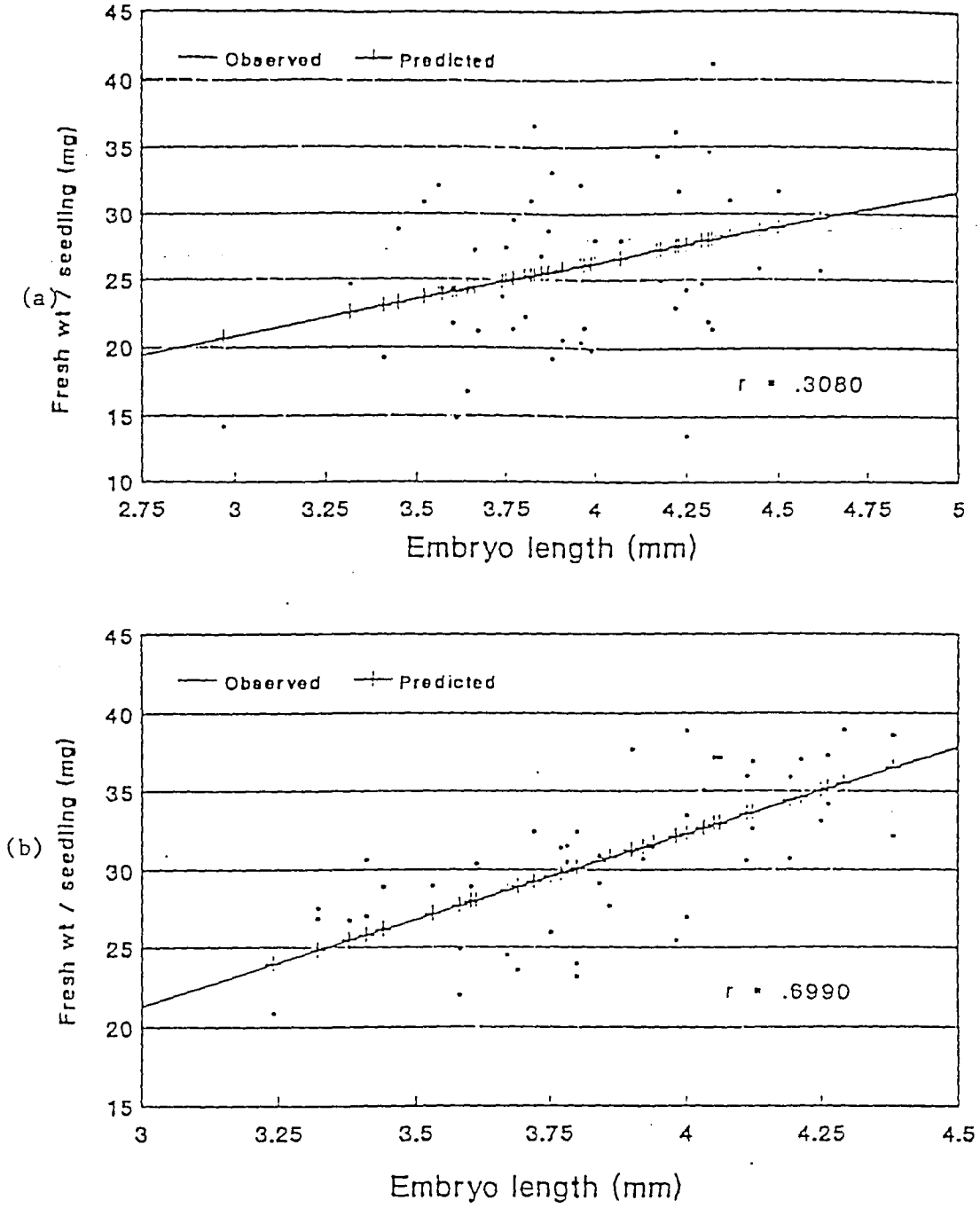


Figure 12 a - b. Relationship between embryo length and seedling weight of Abies balsamea (L.) Mill. collected in (a) 1987 and (b) 1988.

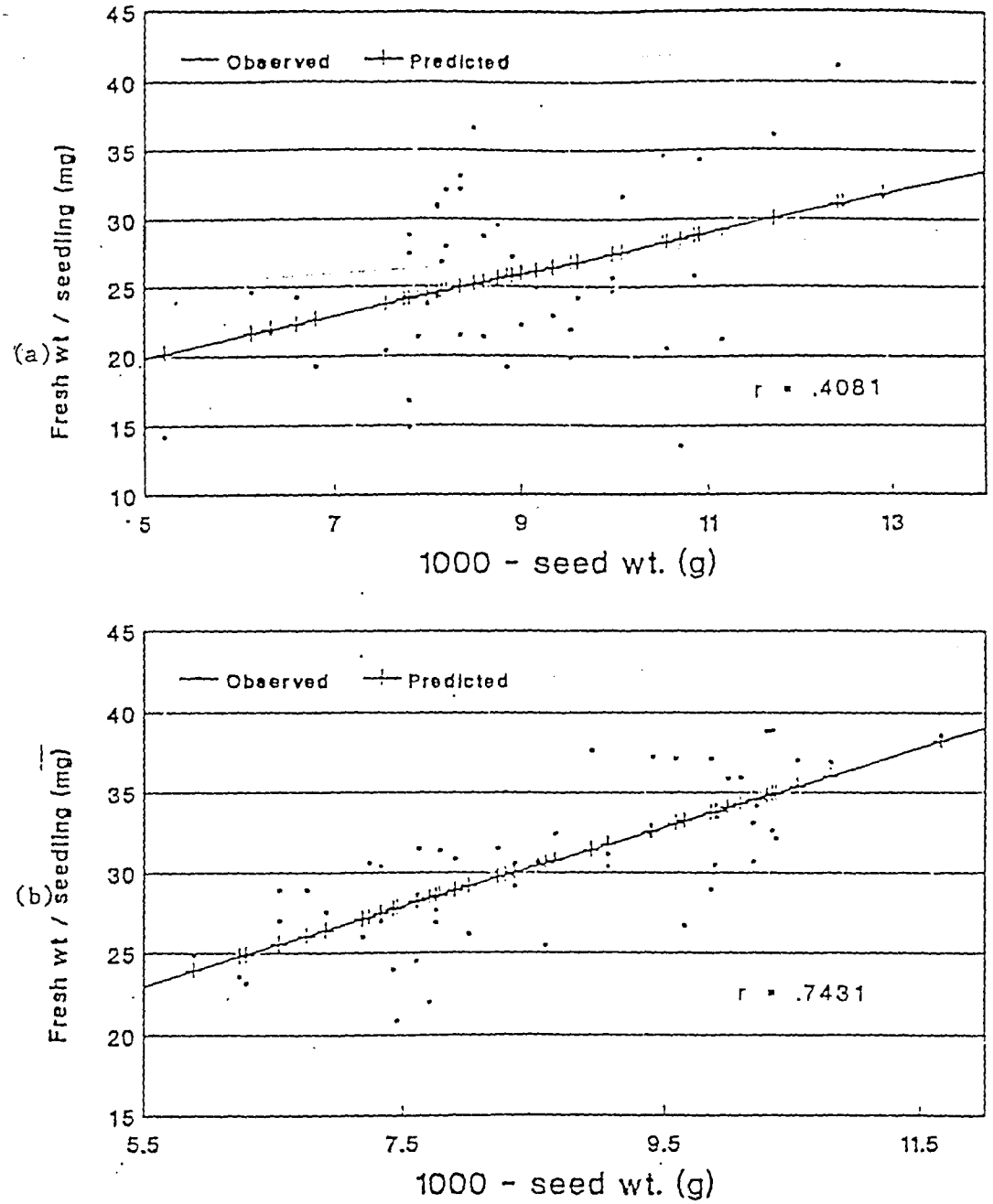


Figure 13.a - b. Relationship between 1000-seed weight and seedling fresh weight of Abies balsamea (L.) Mill. collected in (a) 1987 and (b) 1988.

Table 18. Correlations between leachate conductivity and other physiological characters of balsam fir.

	Leachate conductivity	
	1987	1988
% Normal germination	-0.2963[a/]*	-0.4140**
	0.0329[b/]	0.0023
	52[c/]	52
Peak value	-0.2882*	-0.2383[NS]
	0.0383	0.0890
	52	52
Germination value	-0.2685*	-0.3043*
	0.0543	0.0283
	52	52
Mean daily germination	-0.2807*	-0.4084**
	0.0439	0.0027
	52	52

a/ Correlation coefficient (r)
b/ p - value
c/ Number of observations

* Significant
** Highly significant

Table 19. Correlations between physical and physiological characters of balsam fir, 1987-1988.

	Embryo length		1000-seed wt.		Fresh wt/seedling	
	1987	1988	1987	1988	1987	1988
% Normal germination	NS	NS	NS	NS	0.5943** 0.0001 52	NS
Peak value	NS	NS	NS	-0.3085[a/]* 0.0261[b/] 52 [c/]	0.6020** 0.0001 50	NS
Germination value	NS	NS	NS	NS	0.6089** 0.0001 50	NS
Mean daily germination	NS	NS	NS	NS	0.5795** 0.0001 50	NS
Leachate conductivity	NS	NS	NS	NS	NS	-0.0659 0.6395 53

a/ Correlation coefficient (r)
b/ p - value
c/ Number of observations

* Significant
** Highly significant
ns Non significant at p=≥.05 level.

D. Correlations Between Seed Quality and Stand Characteristics

Only 1000-seed weight (r=0.2712) and seedling fresh weight (r=0.2989) of 1988 seed lots were found to be significantly correlated with tree height (p=0.05). No other significant relationships were found between seed quality and stand characteristics (Table 20).

E. Prediction of Seed Quality

None of the stand characteristics measured and included in the full model could predict any of the seed quality variables; all R-squares obtained were extremely low (Table 21).

F. Correlations Between Seed Quality and Geographic Locations

Seed weight, PV and GV of 1988 seed lots were consistently and significantly correlated with elevation, longitude and latitude (Table 22). Seed weight was correlated negatively with elevation and longitude, but positively with latitude. The other two parameters, however, were correlated with geographic coordinates in the opposite direction. Embryo length was the only seed quality criteria that was not significantly influenced by either elevation, longitude, or latitude (Table 22). Elevation was positively significantly associated with PNG, PV, MDG, GV and seedling fresh weight (1987), but negatively associated with the size of the cone crop

Table 20. Correlations between quality of seed and characteristics of balsam fir trees (seed source).

	Age		DBH		Height		% Defoliation	
	1987	1988	1987	1988	1987	1988	1987	1988
% Normal Germination	NS	---	NS	NS	NS	NS	NS	---
Peak Value	NS	---	NS	NS	NS	NS	NS	
Germination Value	NS	---	NS	NS	NS	NS	NS	---
Mean Daily Germination	NS	---	NS	NS	NS	NS	NS	---
Leachate Conductivity	NS	---	NS	NS	NS	NS	NS	---
Embryo length	NS	---	NS	NS	NS	NS	NS	---
1000 - Seed Wt.	NS	NS	NS			0.2712[a] 0.0495[b] 53[c]	NS	---
Fresh Wt. Seedling			NS	NS	NS	0.2989* 0.0297 53	NS	---

a/ Correlation coefficient ( )
b/ p-value
c/ Number of observations

* Significant at .05 level of probability
NS Non significant (p=>.05)
--- No data

Table 21. Summary of regression analysis of full model equation of balsam fir seed quality.

Response variable (Y)		Predictor variable (X)	Sample size	R^2	$C_{(p)}$	F_{cal}	Prob > F^{NS}
% Normal germination	1987	$X_1 \ldots X_6$	34	0.1150	7.0	0.61	0.7231
	1988	$X_2 \ldots X_3$	51	0.0489	3.0	1.26	0.2926
Peak value	1987	$X_1 \ldots X_6$	34	0.1401	7.0	0.76	0.6070
	1988	$X_2 \ldots X_3$	51	0.0127	3.0	0.31	0.7320
Germination value	1987	$X^1 \ldots X^6$	34	0.1625	7.0	0.91	0.5052
	1988	$X_2 \ldots X_3$	51	0.0081	3.0	.020	0.8186
Embryo length	1987	$X_1 \ldots X_6$	32	0.2133	7.0	1.18	0.3497
	1988	$X_2 \ldots X_3$	52	0.0149	3.0	0.38	0.6865
Leachate conductivity	1987	$X_1 \ldots X_6$	34	0.2631	7.0	1.67	0.1663
	1988	$X_2 \ldots X_3$	52	0.0808	3.0	1.38	0.2612
1000-seed wt.	1987	$X_1 \ldots X_6$	33	0.2293	7.0	1.34	0.2746
	1988	$X_2 \ldots X_3$	52	0.0974	3.0	2.20	0.1215
Fresh wt/ seedling	1987	$X_1 \ldots X_6$	32	1.2684	7.0	1.59	0.1899
	1988	$X_2 \ldots X_3$	52	0.0974	3.0	2.70	0.0771

Y Seed quality variables
NS Nonsignificant
X_1 = Age
X_2 = DBH
X_3 = Ht
X_4 = % Defoliation
X_5 = Basal
X_6 = Radial

Table 22. Correlations between seed quality of balsam fir and stand locations.[a/]

Seed Characters	Elevation		Longitude		Latitude	
	1987	1988	1987	1988	1987	1988
Embryo length	NS	NS	NS	NS	NS	NS (-)
1000 - seed	NS	-.5090[b/]** .000[c/] 53[d/]	NS	-.4113** .0021 53	-.2729* .0480 53	.3715** .0062 53
Fresh wt/seedling	.3465* .0193 51	NS (-)	.3372* .0106 51	NS	NS	NS (-)
% Normal germaination	.3235* .0193 52	NS	.3515* .0106 52	NS	NS	NS (-)
Peak value	.3183* .0215 52	.3995** .0033 52	.3892** .0043 52	.4051** .0029 52	NS	-.3864** .0047 52
Gremination value	.3779** .0057 52	.2912* .0362 52	.4193** .0020 52	.3545** .0099 52	NS	-.3569** .0094 52
Mean daily germination	.3003* .0305 52	NS	.3279* .0176 52	NS	NS	NS (-)
Leachate conductivity	NS (-)	NS	NS (-)	NS (-)	-.3930** .0033 54	.3281* .0165 58
Cone crop size	-.5409** .0003 40		NS		NS	

[a/] Exact locations are in Table 1
[b/] Simple correlation coefficient
[c/] p-value
[d/] number of observations

** Highly significant at ≤.01 level of probability
* Significant at .05 level of probability
NS Non significant (p>.05)

(r=-0.5409) in 1987 and 1000-seed weight (r=-0.5090) of 1988 lots (Table 22). Strength of association of some seed qualities with geographic coordinates of seed source varied from year to year (Table 22).

Abies fraseri (Pursh) Poir.

A. Physical Characteristics

Percent filled and resin-filled seed. Clingman's Dome and Roan Mountain seed lots had about twice as many filled as resin-filled seeds in 1986, but differences between lots were not significant (Table 23). Collections in 1987, however, differed significantly in this characteristic. Mount Mitchell lots exhibited an extremely low percent of filled seed (17.8 percent) and a high (85.6 percent) resin filled fraction (Table 23). It is evident that significant differences (p=0.01) in filled and resin filled seed existed among these 1987 seed lots.

1000-seed weight. The weight of 1000 seeds ranged from 10.01 to 10.33 g and 10.40 to 11.90 g in 1986 and 1987, respectively (Table 24). Clingman's Dome and Roan Mountain seeds were equal in weight in 1986. There were slight differences among the 1987 collections, but differences among lots were nonsignificant in both years. Within seed lots, however, seed weights were all highly significantly different (p=0.01).

Embryo length. The length of embryos was basically the same among seed lots in both years (1986 and 1987);

Table 23. Mean percent filled and resin-filled Fraser fir seeds, 1986-1987*

Collection site	Filled (%)	Resin filled (%)
1986**		
Clingman's Dome, Tenn.	68.7	31.3
	(3.7)	(3.6)
Roan Mt., N. C.	57.5	31.3
	(4.4)	(5.7)
1987		
Mt. Rogers, Va.	74.8 a	25.3 b
	(5.5)	(3.9)
Canaan Valley RA, W.Va.	67.6 a	32.4 b
	(5.7)	(4.3)
Mt. Mitchell, N. C.	17.8 b	85.6 a
	(6.1)	(4.4)

* Each mean represents 9-15 sampled trees and 4 subsamples per tree.

** No significant difference at .05 level of probability. Analyses of variance are in Tables 46-49 of the Appendix. Means followed by same letter in same year and column are not significantly different at .05 level of probability. Number in parenthesis is standard error.

Table 24. Mean weight of 1000-Fraser fir seed, embryo length, and seedling fresh weight, 1986-1987*

Collection site	Seed wt (g)	Embryo length (mm)	Seedling fresh wt. (mg)
1986**			
Clingman's Dome, Tenn.	10.3	4.3	35.1
	(0.3)	(0.1)	(1.5)
Roan Mt., N. C.	10.0	4.3	36.4
	(0.3)	(0.1)	(1.6)
1987**			
Mt. Mitchell, N. C.	11.9	4.4	31.60
	(0.6)	(0.1)	(2.1)
Canaan Valley RA, W.Va.	11.8	4.3	35.8
	(0.5)	(0.1)	(1.8)
Mt. Rogers, Va.	10.4	4.3	31.3
	(0.5)	(0.1)	(1.8)

* Each mean represents 9-15 sampled trees and 4 subsamples per tree.

** No significant difference at .05 level of probability. Analysis of variance of seed wt, seedling wt, and embryo length are in Tables 50-51, 52-53, and 54-55 of the Appendix.

longest and shortest embryo lengths differed by 0.13 mm only (Table 24). No significant difference was found among seed lots in either year. Highly significant differences (p=0.01) in embryo length existed among samples within seed lots in both years, however.

Seedling fresh weight. Seedling fresh weight ranged from 35.1 to 36.4 mg in 1986, and 31.3 to 35.8 mg in 1987 (Table 24). There was minimal seedling weight difference observed in both years. These differences were not significant among seed lots in the same year, but were highly significant among samples within seed lot. Coefficients of variation of both years were practically the same: 10.57 percent (1986) and 10.61 percent (1987).

B. Physiological Characteristics

Percent normal germination. Germination was poor in both years, but lots of 1987 were physiologically better than those of 1986 (Table 25). Values in 1986 were 25.3 and 33.3 percent, while those of 1987 ranged from 43.0 at Mt. Mitchell to 57.5 percent at Canaan Valley RA. Differences among seed lots within the same year, however, were found to be nonsignificant in both years (p=0.3 and 0.4). Seed lots in 1986 had about two times higher coefficients of variation than 1987 (29.36 vs. 14.54 percent). Seed lots from primary and secondary sites were comparable in their germination capacity.

Peak value, Mean daily germination, and Germination value. Based on PV, MDG, and GV, 1987 seeds were of much higher quality than those of 1986 (Table 25). The latter seed lots had PV's that ranged from 1.5 to 1.8, MDG's of 1.2 to 1.5 and GV's of 2.6 to 3.6, while 1987 values were about double those. No statistical difference was observed in PV, MDG, or GV among seed lots in either 1986 or 1987. It was observed, however, that samples within seed lots in either year were significantly different ($p=0.01$). Based on these responses, seed lots from the primary sites basically had germination behavior comparable to seeds from secondary sites.

Leachate conductivity. Leachate conductivity levels of 1986 lots (<91 μA) were much lower than those of the succeeding year (<139 μA) (Table 26). Differences among seed lots in 1986 and 1987 were significant ($p=0.04$) and nonsignficiant ($p=0.2$), respectively.

Response to accelerated aging test. Germination of all lots decreased as days of aging increased. However, the rate of decline differed among seed lots (Figure 14 a and b). Separation of seed quality was more evident in the 1986 lots than in those of 1987. The greatest difference in response was after two days of aging in 1986 lots and after four days in the 1987. Roan Mt., North Carolina seeds showed stimulation on the second day of aging but declined rapidly on the fourth day. Germination of all seed lots irrespective of collection year dropped

Table 25. Mean percent normal germination, peak value, mean daily germination, and germination value of Fraser fir, 1986-1987*

Collection site	PNG	PV	MDG	PV
1986**				
Roan Mt, N. C.	33.3	1.8	1.5	3.6
	(4.1)	(0.3)	(0.2)	(0.8)
Clingman's Dome, Tenn.	25.3	1.5	1.2	2.6
	(3.9)	(0.2)	(0.2)	(0.7)
1987**				
Canaan Valley RA, W.Va.	57.5	3.1	2.7	9.5
	(6.3)	(0.3)	(0.3)	(1.7)
Mt. Rogers, Va.	54.1	2.9	2.6	8.3
	(6.3)	(0.3)	(0.3)	(1.7)
Mt. Mitchell, N. C.	43.4	2.4	2.1	6.2
	(7.3)	(0.4)	(0.3)	(2.0)

* Each mean represents 9-15 sampled trees and 4 subsamples per tree.

** Not significant difference at .05 level of probability. Analyses of variance of PNG, PV, MDG, and GV are in Tables 56-67, 58-59, 60-61, and 62-63 of the Appendix, respectively. Number in parenthesis is standard error.

Table 26. Mean leachate conductivity of Fraser fir, 1986-1987*

Collection site	Leachate Conductivity (uA)	
1986		
Clingman's Dome, Tenn.	90.5 (1.7)	a
Roan Mt, N. C.	85.2 (1.8)	b
1987**		
Mt. Mitchell, N. C.	137.7 (3.1)	
Mt. Rogers, Virginia	134.0 (2.6)	
Canaan Valley RA, W.Va.	130.3 (2.6)	

* Each mean represents 9-15 sampled trees and 4 subsamples per tree.

** No significant difference at .05 level of probability.

Means followed by same letter in same year and column are not significantly different at .05 level of probability.

Analyses of variance are in Tables 64-65 of the Appendix.

Number in parenthesis is standard error.

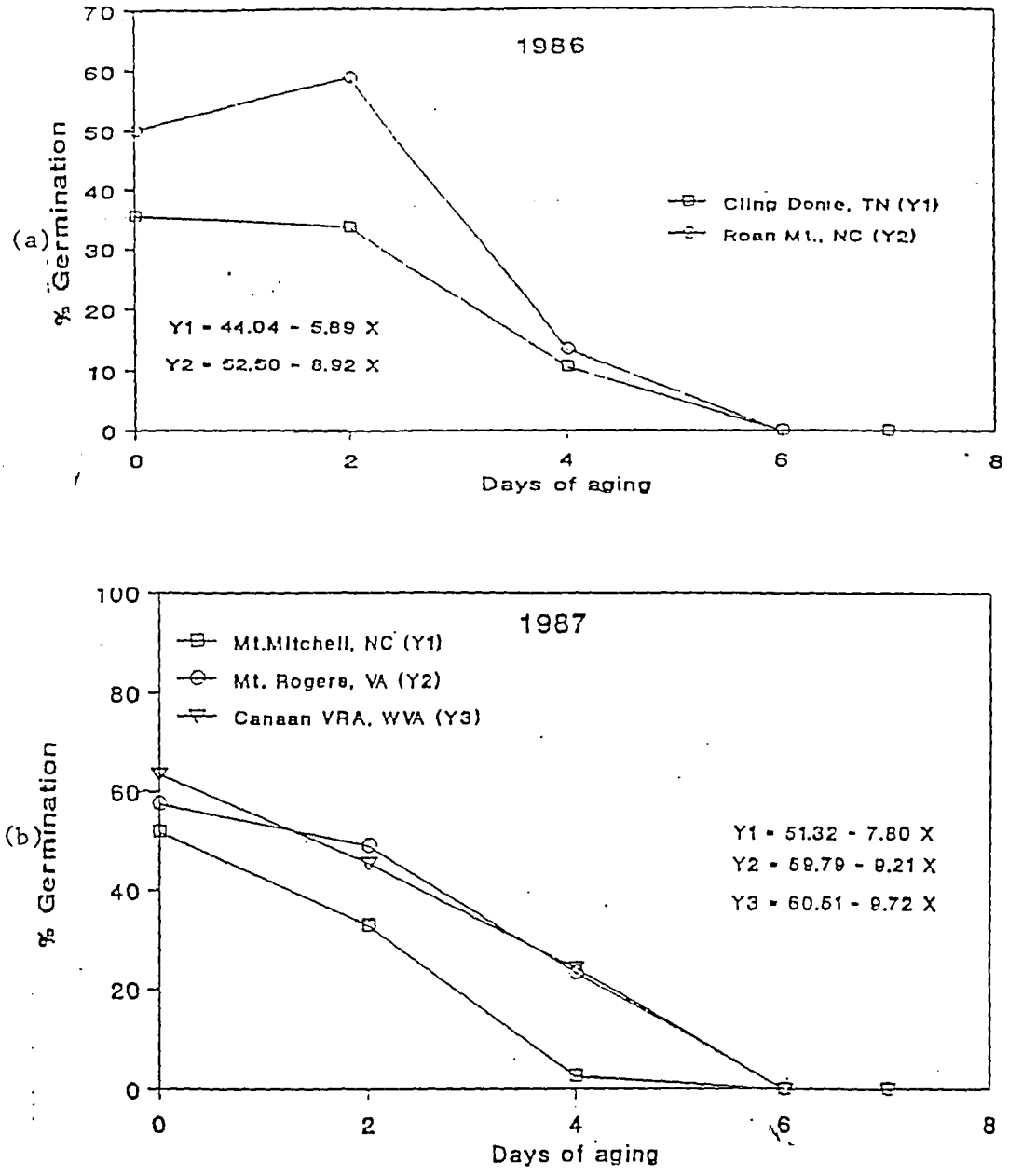


Figure 14 a - b. Germination responses of Abies fraseri (Pursh) Poir. to accelerated aging test.

to zero after six days of accelerated aging. Based on this test, Roan Mt. (1986), a secondary site and Mt. Rogers (1987), a primary site, were the best seed lots, as they exhibited more tolerance to temperature stress after two days of aging (Figure 14 a and b).

Response to germination temperature. All seed lots (1986 and 1987) germinated in a wide range of temperature regimes within the range of 9°-32°C. The 1986 lots (Figure 15) were more tolerant of sub (<14°C) and supraoptimal (>32°C) temperatures than the 1987 seeds (Figure 16).

Highest germination percentage (1986 and 1987 seed lots) was exhibited in an alternating temperature range of 20°-24°C (16 hours) and 14°-20°C (8 hours). Rapid germination was observed in long (16 hours) warm (24°-32°C) temperatures, but it was slower with colder nights and days (Figures 15 and 16).

Roan Mt. seeds (secondary site) germinated better than seeds from Clingman's Dome (primary site) in almost all temperature regimes above 9°C (Figure 15). Seed lots from Canaan Valley RA and Roan Mt., both secondary sites, appeared to be most adaptable to wider temperature ranges. The 1987 lots were more sensitive to long (16 hours) warm (32°-38°C) and cold (9°-14°C) temperatures with decreasing or increasing day temperatures than 1986 lots.

Temperatures found to be detrimental to all seed lots were constant cold (9°-14°C) and warm (32°-38°C) and

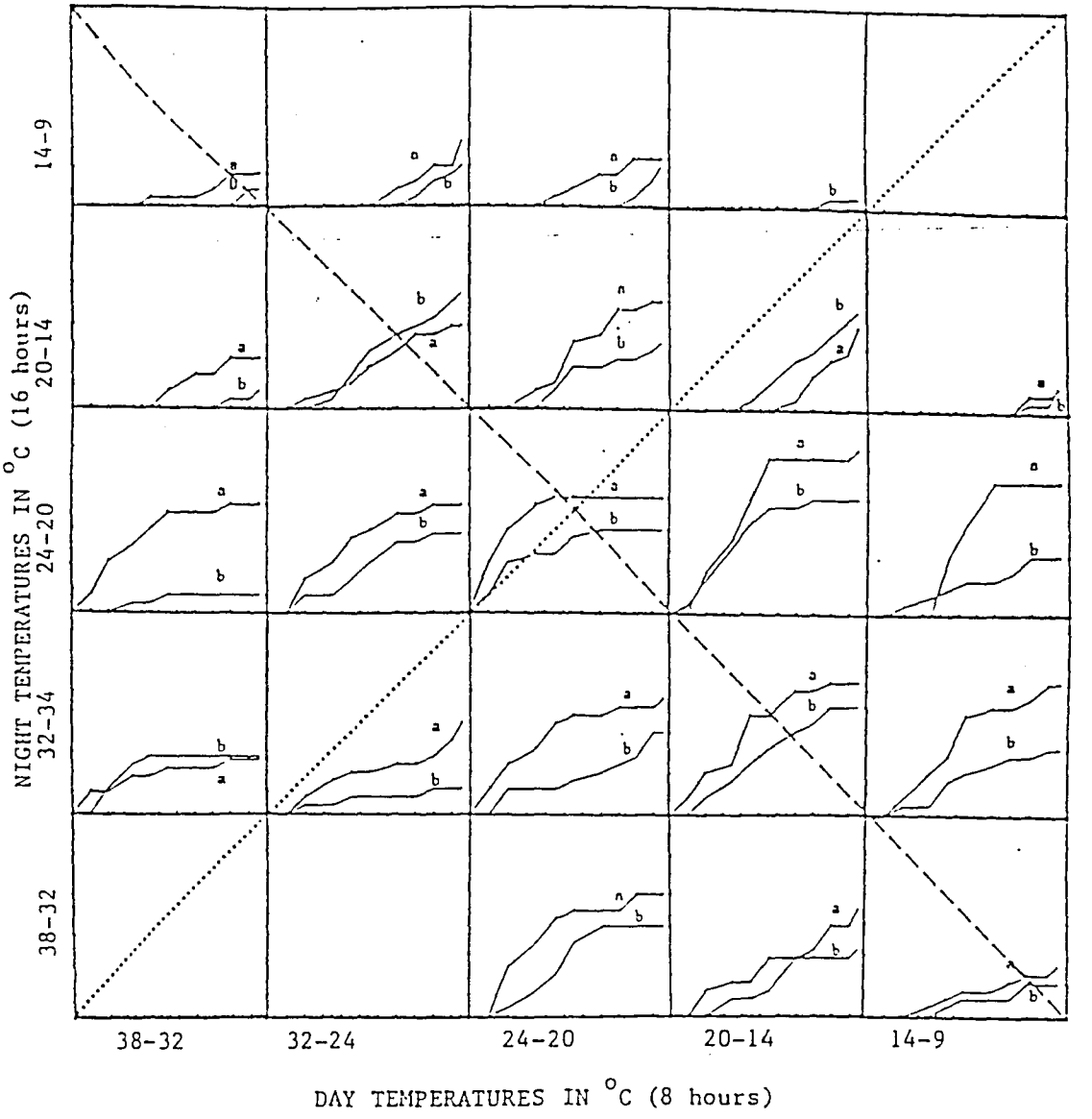


Figure 15. Top view of a two-way Thermogradient table showing germination responses of Abies fraseri (Pursh) Poir. seed lots in 1986. Each temperature regime is represented in cells. Each cell has 2-day germination count intervals (X-axis) and 10 percent total germination capacity intervals (Y-axis). Legend: (a) Roan Mt.; (b) Clingman's Dome; (...) constant temperature; (---) alternating temperature.

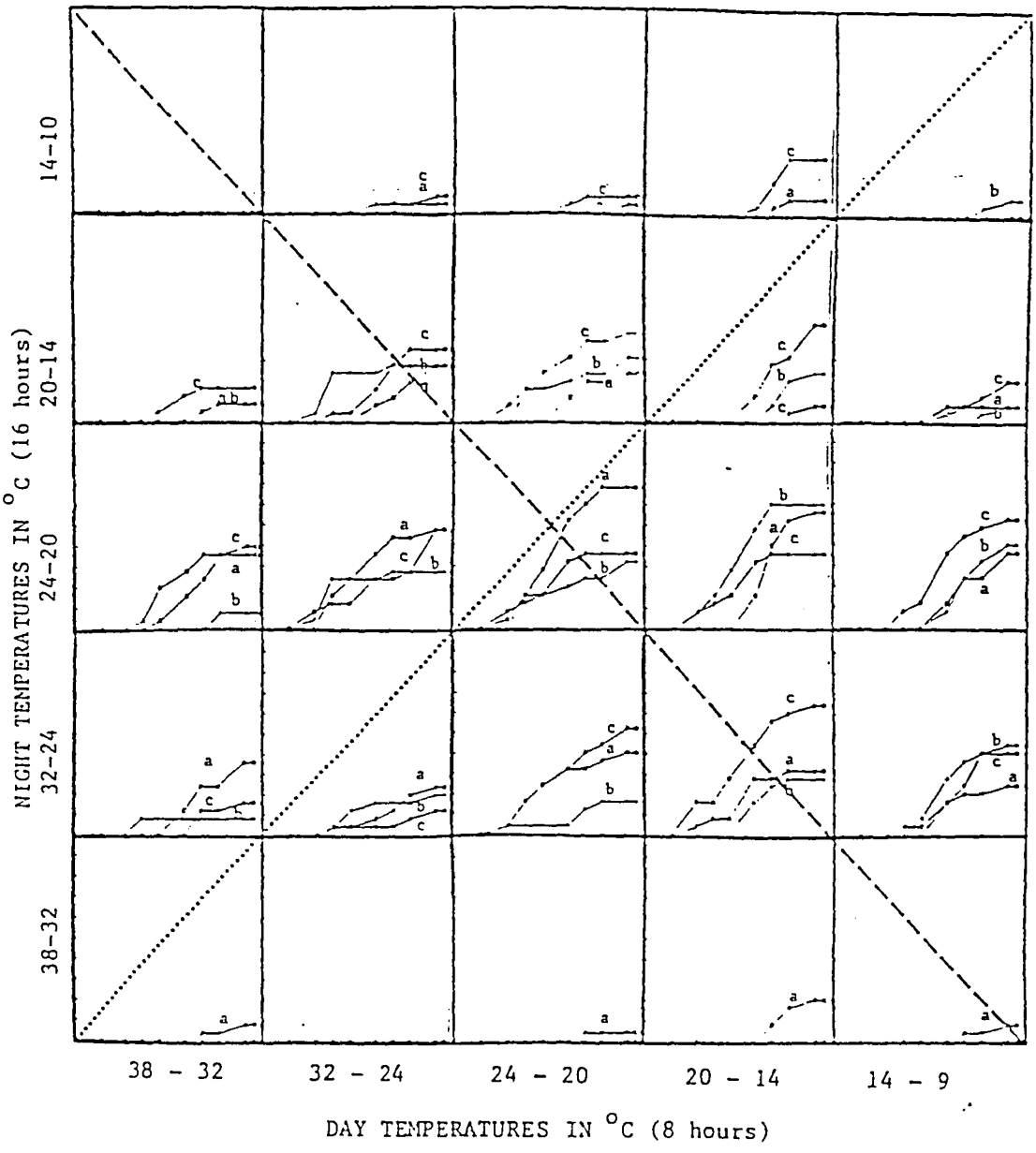


Figure 16. Top view of a two-way Thermogradient table showing germination responses of Abies fraseri (Pursh) Poir. seed lots in 1987. Each temperature regime is represented in cells. Each cell has 2-day germination count intervals (X-axis) and 10 percent total germination intervals (Y-axis). Legend: (a) Mt. Rogers; (b) Mt. Mitchell; (c) Canaan Valley RA; (...) constant temperature; (---) alternating temperature.

alternating nearly warm (32°-38°C) and cold (9°-14°C) temperatures with 24°-32°C (day) temperature and 14°-20°C (night), respectively. Seed lots from primary sites responded porly in most of the temperature regimes as compared to lots from secondary sites.

C. Correlations Among Seed Quality Characters

Significant relationships were observed between embryo length with 1000-seed weight (r=0.8038 and 0.7315) (Figure 17 a and b) and seedling fresh weight (r=0.5869 and 0.4189) (Figure 18 a and b), and between seed weight and seedling fresh weight (r=0.5450) (Figure 19 a and b). Percent filled and resin filled seed were found to be weakly associated with other physical seed characters (Table 27). These two parameters, however, were highly and negatively correlated (r=-0.9998). This is due to the cleaning and upgrading processes that remove empty seeds and debris and make density separations prior to evaluation (Figure 1).

Among physical seed characters, only seedling fresh weight was consistently significantly correlated with physiological characteristics of seed: PNG (r=0.3507 and 0.4337), PV (r=0.3949 and 0.4662), GV (r=0.4864, 1987 only), and MDG (r=0.3495 and 0.4331) (Table 28). As expected, percent filled and percent resin-filled seed were positively and negatively correlated, respectively, with percent PNG and MDG of 1987 seed lots. Other relationships were weak (Table 28).

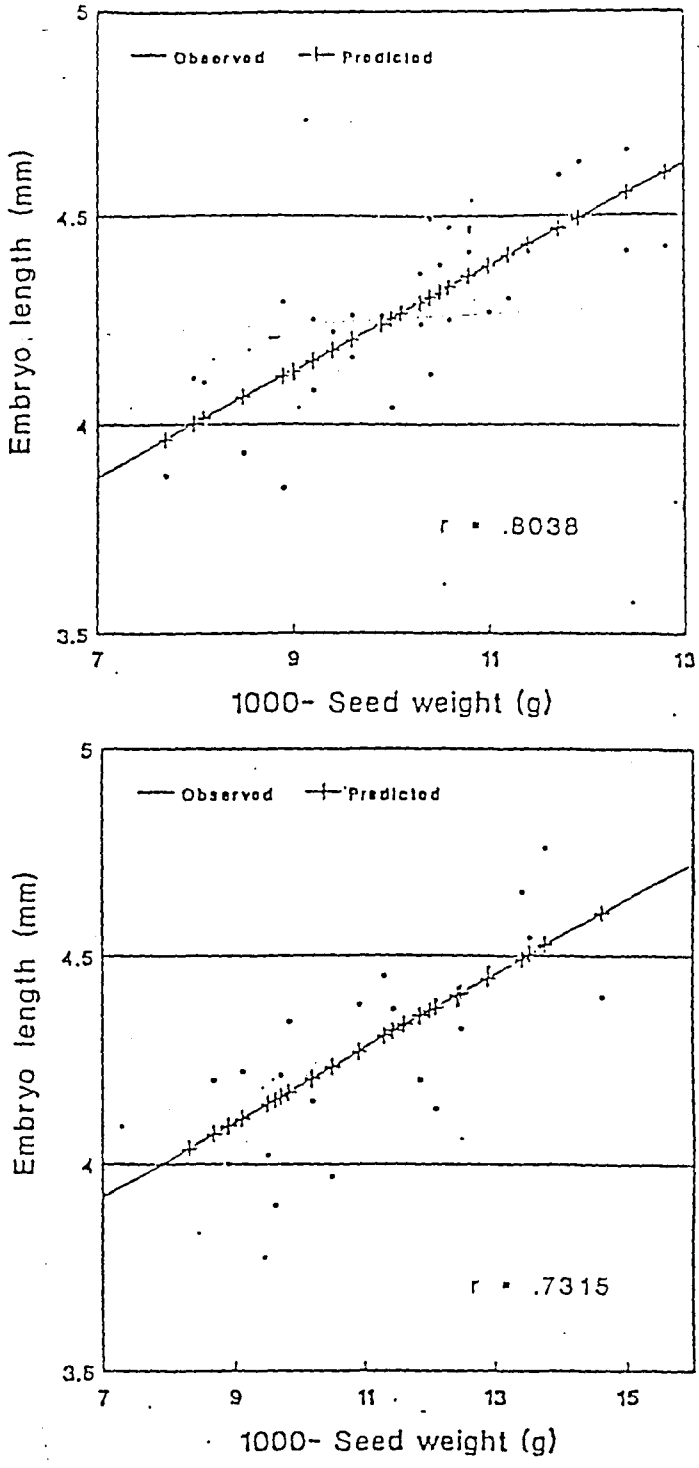


Figure 17 a - b. Relationship between 1000-seed weight and embryo length of Abies fraseri collected in (a) 1986 (b) 1987.

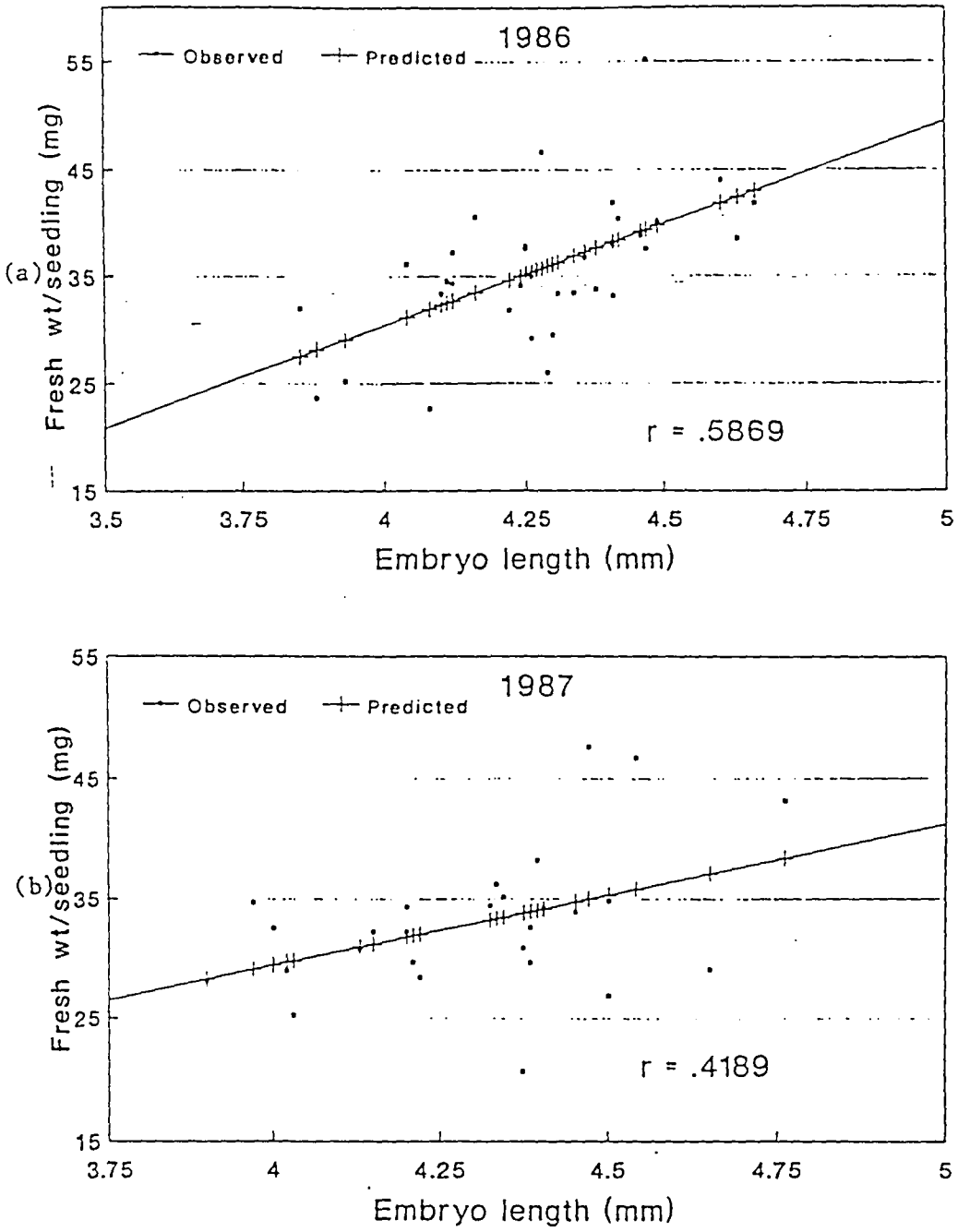
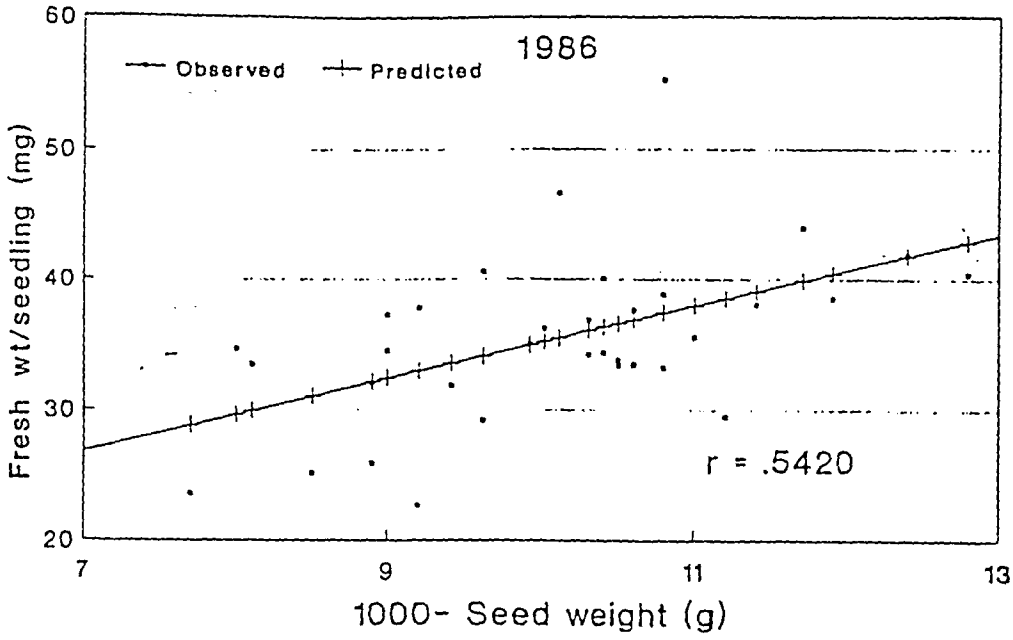


Figure 18 a - b. Relationship between embryo length and seedling fresh weight of Abies fraseri (Pursh) Poir. collected in (a) 1986 and (b) 1987.



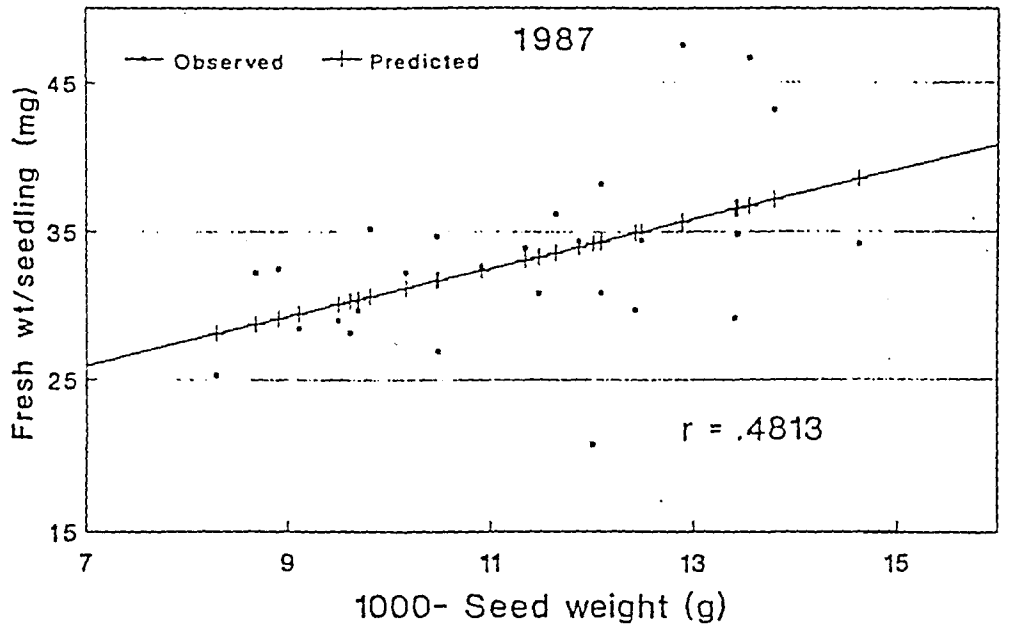


Figure 19 a - b. Relationship between 1000-seed weight and seedling fresh weight of Abies fraseri (Pursh) Poir. collected in (a) 1984 and (b) 1987.

Table 27. Correlations between physical characteristics of Fraser fir seed lots, 1986 - 1987

	Embryo length		1000 - seed wt.		Fresh wt./seeling		% filled seed	
	1986	1987	1986	1987	1986	1987	1986	1987
Embryo length	--	--						
1000-seed wt.	0.8038[a/]** 0.0001[b/] 36 [c/]	0.7315** 0.0001 27	--	--				
Fresh wt/seedling	0.5869** 0.0002 36	0.4189** 0.0297 27	0.5450** 0.0006 36	0.4813** 0.0095 28	---	---		
% Filled seed	NS	NS	NS	NS	NS	NS	---	---
% Resin-filled seed	NS	NS	NS	NS	NS	NS	NS	0.9998** 0.0001 36

** Highly significant

a/ Correlation coefficient (r)

b/ p-value

c/ Number of observations

Table 28. Correlations between physical and physiological characters of Fraser fir seed lots.

	% Normal Germination		Peak Value		Germination Value		Mean Daily Germination		Leachate Conductivity	
	1986	1987	1986	1987	1986	1987	1986	1987	1986	1987
Embryo length	-0.0314[a]	0.1875	-0.0457	0.1195	-0.0946	0.2069	-0.0318	0.1877	0.3775*	0.2762
	0.8558[b]	0.3490	0.7913	0.5527	0.5833	0.3003	0.8541	0.3484	0.0232	0.1632
	36[c]	27	36	27	36	27	36	27	36	27
1000-seed wt	-0.1405	0.0684	-0.1739	-0.0090	-0.2430	0.0494	-0.1415	0.0688	0.2040	0.2731
	0.4139	0.7293	0.3105	0.9600	0.1533	0.8027	0.4104	0.7280	0.2326	0.1597
	36	28	36	28	36	28	36	28	36	28
Fresh wt/ seedling	0.3507*	0.4337*	0.3949**	0.4662**	0.2906	0.4864**	0.3495*	0.4331*	0.0443	0.1063
	0.0360	0.0211	0.0171	0.0124	0.0856	0.0087	0.0367	0.0213	0.7975	0.0568
	36	28	36	28	36	28	36	28	36	28
% Resin filled seed	-0.0122	-0.4058*	0.0261	-0.3508	-0.0380	-0.3595	-0.0134	-0.4052*	0.1019	0.3710*
	0.9439	0.0357	0.8799	0.0728	0.8259	0.0655	0.9383	0.0360	0.5543	0.0568
	36	27	36	27	36	27	36	27	36	27
% filled seed	0.0063	0.4058*	-0.0323	0.3508	0.0310	0.3595	0.0075	0.4052*	-0.1013	-0.3710*
	0.9709	0.0357	0.8515	0.0728	0.8575	0.0655	0.9654	0.0360	0.5568	0.0568
	36	27	36	27	36	27	36	27	36	27
Leachate conductivity	0.3518*	-0.3812*	-0.3166*	-0.3427	-0.3109	-0.3013	-0.3513*	-0.3823*		
	0.0354	0.0453	0.0600	0.0743	0.0649	0.1192	0.0357	0.0447	---	---
	36	28	36	28	36	28	36	28		

* Significant at .05 level of probability.
** Highly significant at .01 level of probability.
[a] correlation coefficient ( ).
[b] p-value
[b] Number of observations.

Correlations between leachate conductivity and physiological seed characters (PNG, PV, MDG, GV) were consistently negative (Table 28). However, the association became positive when leachate conductivity was correlated with the physical seed characters (excluding percent filled and resin-filled seed criteria).

D. Correlations Between Seed Quality and Stand Characteristics

Poor association was found between seed quality and stand characteristics (Table 29). Significant correlations were only evident between the percent filled and resin-filled seed with age (1986), DBH (1986), basal area (1987), and radial increment (1987). Physiological seed qualities (PNG, PV, MDG, and GV) were negatively correlated with crown defoliation and positively correlated with cone crop size in 1986. The other relationships were found to be nonsignificant (Table 29). Average seedling fresh weight was found to be highly correlated with the basal area ($r=0.6095$) and radial increment ($r=0.6450$), but the same relationship was not evident in other years (1987).

E. Correlations Between Seed Quality and Geographic Coordinates of Seed Sources

Strong significant correlations were indicated between percent filled and resin-filled seed and all geographic coordinates (elevation, longitude and latitude)

Table 29. Correlations between quality of seed and stand characteristics of Fraser fir.

	Age		DBH		Height		Basal area		Radial Increment		Defoliation		Cone Produced	
	1986	1987	1986	1987	1986	1987	1986	1987	1986	1987	1986	1987	1986	1987
% Normal Germination	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-0.3509* 0.0359 36	NS	0.3684* 0.0295 35	NS
Peak Value	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-0.3327* 0.0474	NS	0.3722* 0.0277	NS
Germination Value	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.3898* 0.0206 35	NS
Mean Daily Germination	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-0.3515* 0.0355 36	NS	0.3692* 0.0291 35	NS
Leachate Conductivity	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Embryo length	NS	NS	NS	NS	NS	-0.4697* 0.0424 19	NS	NS	NS	NS	NS	NS	NS	NS
1000 - Seed Wt.	NS	NS	NS	NS	NS	-0.3386 0.9238 20	NS	NS	NS	NS	NS	NS	NS	NS
Fresh Wt. Seedling	NS	NS	NS	NS	NS	NS	0.6095 0.0073 18	NS	0.6450 0.0038 18	NS	NS	NS	NS	NS
% Resin filled seed	0.5704** 0.0134 18	NS	0.5195** 0.0012 36	NS	NS	NS	NS	0.5707** 0.0107 19	NS	0.46671* 0.0440 19	NS	NS	NS	NS
% Filled seed	-0.5704 0.0134 18	NS	-0.5229 0.2773 36	NS	NS	NS	NS	NS	-0.5707 0.0107 19	NS	-0.4667 0.0440 19	NS		

(Table 30). The direction of association however, varied depending on year of collection. For unknown reasons, leachate conductivity of 1986 seed lots was found to be significantly correlated with elevation (r=0.3428), longitude (r=0.3428), and latitude (r=0.4328) (Table 30).

F. Prediction of Seed Quality

None of the stand characteristics that are included in the linear regression model can predict any of the seed quality criteria (Table 31).

Table 30. Correlations between seed quality of Fraser fir and stand locations.[a/]

Seed characters	Elevation		Longitude		Latitude	
	1986	1987	1986	1987	1986	1987
Embryo length	NS	NS	NS	NS	NS	NS
1000-seed wt	NS	NS	NS	NS	NS	NS
Fresh wt/seedling	NS	NS	NS	NS	NS	NS
% filled seed	.3312[b/]*	-.4161*	.3312*	-.7408**	-.3312*	.5379**
	.0485[c/]	.0309	.0485	.0001	.0485	.0038
	36[d/]	27	36	27	36	27
% Resin filled seed	-.3277*	.4161*	-.3277*	.7408**	-.3277*	.5379**
	.0511	.0309	.0511	.0001	.0511	.0038
	36	27	36	27	36	27
% Normal germination	NS	NS	NS	NS	NS	NS
Peak value	NS	NS	NS	NS	NS	NS
Germination value	NS	NS	NS	NS	NS	NS
Leachate conductivity	.3428*	NS	.3428	NS	.3428	NS
	.0407		.0407		.0407	
	36		36		36	

[a/] Exact location is found in Table 1
[b/] Correlation coefficient
[c/] p-value
[d/] Number of observations
NS Nonsignificant at p=.05 level.

Table 31. Summary of regression analysis of full model equation of Fraser fir seed quality.

Response variables (Y)		Predictor variables (X)	Sample	R^2	$C_{(p)}$	F_c	Prob > F
% Normal germination	1986	X_1..... X_7	17	0.5874	8.0	2.03	0.189
	1987	X_1..... X_6	19	0.2774	7.0	0.83	0.5661
Peak value	1986	X_1..... X_7	17	0.5363	8.0	1.65	0.2274
	1987	X_1..... X_6	19	0.3304	7.0	1.07	0.4284
Germination value	1986	X^1..... X^7	17	0.5424	8.0	1.69	0.2170
	1987	X_1..... X_6	19	0.3359	7.0	1.10	0.4148
Embryo lenght	1986	X_1..... X_7	17	0.3670	8.0	0.83	0.5868
	1987	X_1..... X_6	19	0.4417	7.0	1.58	0.2347
1000-Seed wt.	1986	X_1..... X_7	17	0.4799	8.0	1.32	0.3339
	1987	X_1..... X_6	19	0.1842	7.0	0.49	0.8053
Fresh / seedling	1986	X_1..... X_7	17	0.6049	8.0	2.19	0.1265
	1987	X_1..... X_6	19	0.2055	7.0	0.56	0.7544
% Filled seed	1986	X_1..... X_7	17	0.5481	8.0	1.73	0.2075
	1987	X_1..... X_6	19	0.4880	7.0	1.91	0.1608
% Resin filled seed	1986	X_1..... X_7	17	0.5481	8.0	1.73	0.2075
	1987	X_1..... X_6	19	0.4880	7.0	1.91	0.1608
Leachate conductivity	1986	X_1..... X_7	17	0.4410	8.0	1.13	0.4173
	1987	X_1..... X_6	19	0.0845	7.0	0.20	0.9708

X_1 = Age
X_2 = DBH
X_3 = Ht
X_4 = % Defoliation
X_5 = Basal area
X_6 = Radial increment
X_7 = Cone crop size (Est. # of cones)

DISCUSSION

Seed Quality Variations

Variation of cone and seed characterics among trees within populations, among stands or populations of the same species, among geographic locations or sites within a given year, and among collection years have been reported for many species (Ager and Stettler 1983, Baumgartner et al. 1984, Bingham and Rehfeldt 1970, Burdon and Low 1972, Cabala 1982, Calvert 1978, Clausen 1980, Clausen et al. 1981, Fober and Giertych 1971, Heit and Natti 1969, Nienstaedt and Teich 1972, Franklin and Greathouse 1968, Pulliainen and Lajunen 1984, Ryynanen 1982, Rubanik and Parshina 1978, Sorensen and Franklin 1977, Sorensen and Miles 1978). Similar findings were observed in red spruce, balsam fir, and Fraser fir seed lots in the present study. Tree to tree variation in all cone and seed characters was highly significant in all species studied. Some lots (1987 red spruce, 1987 balsam fir and Fraser fir) collected from geographic locations proximal to each other did not differ significantly in most of their seed qualities.

Cone and seed qualities are influenced by genetic and environmental factors, although Rubanik and Parshina (1978) report that cone and seed yields are mainly under genetic influence. Size of red spruce cones exhibited a

geographic trend; smaller and shorter cones were found in the southern-most population in 1987.

Seed yield in red spruce followed a yearly pattern, poor seed yield in 1986, good in the succeeding year (1987), and best in the third year (1988). Poorer seed yields in red spruce generally came from southern sites. This is probably due to the fact that southern sites are found in higher elevations where extreme climatic conditions are likely to occur; or maybe due to pollution (Houston and Dochinger 1977, Bonte 1982, Pelz 1963), as pollution gradient was directly proportional to elevation (Hertel 1988, Mohnen 1988, MacKenzie and El-ashry 1988).

Seed weight, embryo length, and seedling fresh weight also followed a geographic pattern. In 1986 and 1987, red spruce had significantly heavier and longer embryos and heavier seedlings from southern than northern sites. No significant difference was observed in 1988 red spruce, balsam fir (1987 and 1988), and Fraser fir (1986 and 1987) seed lots, as geographic locations of seed sources were confined only in the northern sites on the first two species, and only southern sites on the third (Fraser fir). These conclusions are supported by the consistently high correlations between seed weight and geographic coordinates of seed source in red spruce (Table 13); inconsistent correlation in balsam fir and no significant correlations in Fraser fir. This confirms findings of

Melzack and Watts (1982) and Pitcher (1984) that seed weight displays a clinal pattern.

Resin-filled seeds were only observed in Fraser Fir. Heit (1961) reported the presence of resin-filled seed in Fraser fir, but he did not speculate on any possible cause. This could be due to either genetic or environmental factors. In the 1986 collection there were equal proportions of resin-filled and filled seed, but not in 1987. Mt. Mitchell (1987) seed had an extremely high (85.63 percent) proportion of resin-filled seeds when compared with Roan Mt. seed in 1986 (adjacent site). It seems that environment must have the greatest influence, and the relationship changed with time.

All species exhibited year to year and tree to tree variations in PNG, PV, MDG, and GV. Seed yields were poor in 1986, but good in the succeeding year(s). Red spruce (1987 seed lots), balsam fir (1988 seed lots), and Fraser fir (1987 seed lots) were considered to be of good physiological quality. Low germination percentages have been reported as normal among Abies species (Heit and Natti 1969, Speers 1974, Edwards 1982, Adkins et al. 1984) due to insect and disease damage. Low germination percentages were also found to be normal in this study; however, insect damage was not the cause since insect-infested seeds were removed during conditioning.

Melzack and Watts (1982), Mohan et al. (1984) and Van Haverbeke and Comer (1985) reported that germination

varied among provenances and trees in Taxus baccata L., Leptospermum scoparium, and eastern red cedar, respectively. Results obtained with red spruce and Fraser fir in this study did not strongly agree with their findings, but did for balsam fir. This is shown by the poor correlations obtained between seed characters and geographic coordinate of the collection sites.

Vozzo and Bonner (1985) reported strong correlations between conductivity and standard germination in southern pine species. Similar results were not realized in this study, however. The small size of red spruce seed and the presence of resin adhering to the outer seed coat of the two firs probably caused extreme variation in readings that lead to poor correlations.

Bonner and Vozzo (1986) and Blanche and Elam (1989) reported the potential of accelerated aging tests in the identification of vigorous seed lots. This is a stress test whose basic premise is that high vigor seed lots will only show a slight decline in germination while low vigor lots will decline markedly after certain accelerated aging periods (AOSA 1983). This test was found to be applicable to the three species studied. Most vigorous seed lots were identified at the point where widest separation of response occurred, which was after four days for red spruce and two days for balsam and Fraser firs. Germination of some seed lots in all three species was enhanced. This response, so far unexplained, was also

reported by Blanche et al. (1988) in water oak (Quercus nigra L. and pecan (Carya illinoensis (Wangenh.) K. Koch.

Temperature regimes ranging from 20°-32°C for either 16 and 8 hours, constant or alternating mode, were favorable for red spruce, balsam fir, and Fraser fir germination. Red spruce, unlike the two firs, responded favorably to either constant or alternating temperatures. This supported the alternating germination temperatures recommended for testing by AOSA (1985), but red spruce also performed equally well at constant temperatures.

Thompson (1975), Bonner (1982), Mohan et al. (1984), and Murdoch et al. (1989) found great variability in the germination response of seed lots tested at various temperature regimes. These variations in germination rate and total germination were evident in red spruce, balsam fir and Fraser fir placed in different temperature gradients. Generally, however, germination rate was more affected than total germination. This observation was also reported by Mohan et al. (1984). Temperature thresholds common to all three species were constant cold (9°-14°C) and warm (32°-38°C) temperatures.

Seed Quality Relationships

Fober and Giertych (1971) found significant correlations among seed weight, embryo length, and seedling fresh weight in Norway spruce. The present study shows that these three seed characters were consistently

highly correlated with each other in red spruce, balsam fir, and Fraser fir.

Seedling fresh weights were highly influenced by PNG, PV, MDG and GV in all species. These parameters were negatively correlated with leachate conductivity, but not as strongly as expected. Seed weight was found to be weakly correlated with the physiological parameters, which contradicts the results of others that heavier or bigger seeds germinate faster and produce bigger seedlings (Canido 1970, Barnett and Dunlap 1982, Melzack and Watts 1982, Kim et al. 1987), but agreed with Bonner's (1987) findings in Pinus echinata and P. elliottii.

Wang (1976) noted that germination of white spruce varied greatly in poor to mediocre seed years, but was consistent and uniform in good seed years. This relationship was evident for red spruce, but not for balsam and Fraser firs in this study. Considerable tree to tree variation in seed quality in all species contradicts Ryynanen's (1982) report that great variation ocurred in bad seed years.

Correlations between seed quality characteristics and stand conditions were inconsistent in red spruce and consistently weak in balsam fir and Fraser fir. Seed quality was not strongly influenced by age, diameter, height, basal area, and radial growth of the tree or percent defoliation. These results disagree with Fowells and Schubert's (1956) claim that dominant, large-crowned

trees are the best seed producers, but agree with Varnell's (1976) findings that cone production or seed yields were weakly correlated with d.b.h., height, percent live crown, and tree age.

Geographic locations of seed sources were highly correlated with cone and seed quality in red spruce, but not in balsam and Fraser firs. This may be because red spruce was collected from both northern and southern sites, unlike the firs, whose collections were confined to the north for balsam fir and the south for Fraser fir. Relationships between seed characters and geographic locations are evident in red spruce and balsam fir, but varied from year to year. Percent filled and resin-filled seeds in Fraser fir was significantly correlated with elevation, longitude, and latitude in 1986, but the relationship was reversed in the succeeding year. This change may be due to differing weather conditions in two years. Seed lots from primary sites were comparable to those from secondary sites in all seed quality characters. This is not so in germination response of 1986 Fraser fir seed lots, as a secondary site (Roan Mt.) was consistently superior in almost all temperature regime.

Prediction of Seed Quality

None of the linear regression models could predict seed quality adequately.

SUMMARY AND CONCLUSIONS

Seed Quality Differences Among Populations

The primary objective of this study was to evaluate the quality of seed produced by declining red spruce, balsam fir, and Fraser fir stands in eastern North America. Seeds from 193 red spruce, 107 balsam fir, and 65 Fraser fir trees were sampled from seed lots of 16 (1986, 1987, 1988), 9 (1986, 1987), and 5 (1986, 1987) declining populations of red spruce, balsam fir, and Fraser fir, respectively, in eastern North America.

The following seed quality parameters were measured: cone length and diameter, seed yield, percent filled and non-filled seed, 1000-seed weight, embryo length, seedling fresh weight, percent normal germination, peak value, mean daily germination, germination value, leachate conductivity, response to accelerated aging, and response to germination temperature.

The results from all seed quality criteria determinations showed that:

a. tree to tree variation within seed lots was highly and consistently significant in all collection years for all three species studied;

b. consistent highly significant differences were found among red spruce seed lots collected in 1986 and 1987, but no significant differences were found in the PNG, PV, MDG, GV, and seedling weight of the 1988

collections. Significant variations among balsam fir seed lots were only evident in 1987, but were not apparent in the succeeding year. No difference was found among Fraser fir seed lots collected in both 1986 and 1987, with the exception of percent filled and resin-filled seed in the latter collection.

c. Greatest variability in seed quality of red spruce was evident during the poorest seed year (1986), and decreased during good (1987) to best (1988) seed years. Balsam fir showed the opposite trend, while Fraser fir lots showed no difference between years.

d. Differences in seed vigor among lots could be detected with the accelerated aging test. Maximum differentiation took place after 4 and 2 days of aging at 40±1°C for red spruce and both firs, respectively. Stimulation of germination occurred after two days of aging on some lots of all three species.

e. Seed lots responded differently to different temperature regimes. However, the optimal temperature regime for all species ranged from 20°-24°C in constant or alternating cycles of 8-hour day and 16-hour night. The threshold temperatures common to the species were constant cold (9°-14°C) and constant warm (32°-38°C).

Seed Quality Relationships

a. Correlations among embryo length, 1000-seed weight, and seedling fresh weight were consistently found

to be highly significant in all red spruce, balsam fir, and Fraser fir seed lots. Correlations among other seed quality criteria were significant in only some cases.

b. The degree of associations between seed quality characteristics and condition of the mother trees and between seed quality and geographic locations of seed sources varied according to species and year of collection.

c. Regression model equations derived to predict the seed quality of red spruce, balsam fir, and Fraser fir populations based on stand conditions produced extremely low coefficients of determination (R-square).

Relationship to Stand and Tree Decline

Based on these thirteen seed quality criteria, the following conclusions can be made: poor seed quality was not apparent among all seed lots.

There was no strong evidence for an association between seed quality and elevation of collection sites; hence, no influence of airborne pollutants on seed quality can be inferred.

The variations in seed quality found among and within seed lots could not be described as extreme. This variation could be related to the geographic location of the stands. The 1000-seed weight, embryo length, and seedling weight of all three species were found to be strongly related to seed source. These parameters are

more likely genetic characteristics of the species than the result of environmental influences.

APPENDIX

Appendix Table 1. 1986 Seed yield - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	89.9050	29.9683	8.8858	0.0001
Among trees within sites	48	161.8851	3.3726		

cv = 56.88%

Appendix Table 2. 1987 Seed yield - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	4402.138	733.6897	21.1714	0.0001
Among trees within sites	82	2841.6871	34.6547		

cv = 47.82%

Appendix Table 3. 1988 Seed yield - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	648.821	162.2054	2.84	0.0354
Among trees within sites	43	2453.8373	57.0659		

cv = 54.45%

Appendix Table 4a. 1987 Cone diameter - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	2.2789	0.3798	9.99	0.0001
Among trees within sites	74	2.8131	0.0380	43.79	0.0001
Among samples within trees	223	0.1936	0.0009		

cv = 2.08%

Appendix Table 4b. 1987 cone length - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	30.1159	5.0193	11.60	0.0001
Among trees within sites	74	32.0283	0.4328	36.33	0.0001
Among samples within trees	221	2.6329	0.0119		

cv = 3.27%

Appendix Table 5a. 1988 Cone diameter - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	0.6630	0.1658	3.5341	0.0145
Among trees within sites	41	1.9240	0.0469	117.3171	0.0001
Among samples within trees	135	0.0579	0.0004		

cv = 1.44%

Appendix Table 5b. 1988 Cone length - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	3.8550	0.9638	1.8654	0.1349
Among trees within sites	41	21.1821	0.5166	112.3123	0.0001
Among samples within trees	135	0.6206	0.0046		

cv = 1.93%

Appendix Table 6. 1986 1000-seed weight - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	58.4035	19.4678	20.5803	0.0001
Among trees within sites	49	46.3512	0.9458	11.1946	0.0001
Among samples within trees	159	13.4400	0.0845		

cv = 7.57%

Appendix Table 7. 1987 1000-seed weight - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	29.8245	4.9708	5.3636	0.0001
Among trees within sites	74	68.5798	0.9268	60.5722	0.0001
Among samples within trees	243	3.7137	0.0153		

cv = 3.57%

Appendix Table 8. 1988 1000-seed weight - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	4.6000	1.1500	0.8155	0.5222
Among trees within sites	44	62.0500	1.4102	271.1976	0.0001
Among samples within trees	147	0.7600	0.0052		

cv = 2.27%

Appendix Table 9. 1986 Embryo length - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	7.1479	2.3826	39.5124	0.0001
Among trees within sites	48	2.8957	0.0603	20.10	0.0001
Among samples within trees	156	0.4692	0.0030		

cv = 2.36%

Appendix Table 10. 1987 Embryo length - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	5	2.2176	0.4435	6.8518	0.0001
Among trees within sites	66	4.2722	0.0647	30.8240	0.0001
Among samples within trees	216	0.4642	0.0021		

cv = 2.11

Appendix Table 11. 1988 Embryo length - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	1.3602	0.3401	6.6807	0.0003
Among trees within sites	43	2.1870	0.0509	23.00	0.0001
Among samples within trees	144	0.3184	0.0022		

cv = 2.21%

Appendix Table 12. 1986 Seedling fresh weight - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	1065.2273	355.0758	12.9253	0.0001
Among trees within sites	49	1346.0974	27.4714	17.5100	0.0001
Among samples within trees	159	249.4475	1.5689		

cv = 9.19%

Appendix Table 13. 1987 Seedling fresh weight - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	891.5084	148.5847	8.3542	0.0001
Among trees within sites	74	1316.1332	17.7856	38.2486	0.0001
Among samples within tree	243	112.9925	0.4650		

cv = 4.22%

Appendix Table 14. 1988 Seedling fresh weight - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	167.7182	41.9296	2.2322	0.0809
Among trees within sites	44	826.4829	18.7837	75.0747	0.0001
Among samples within trees	146	35.5350	0.2502		

cv = 3.14%

Appendix Table 15. 1986 Percent normal germination - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	27214.3472	9071.4491	10.0682	0.0001
Among trees within sites	49	44149.1439	901.0029	20.3727	0.0001
Among samples within trees	158	6987.6948	44.2259		

cv = 8.4%

Appendix Table 16. 1987 Percent normal germination - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	6407.7916	1067.9153	15.3766	0.0001
Among trees within sites	74	5139.3622	69.4508	4.3335	0.0001
Among samples within trees	243	3894.4513	16.0265		

cv = 4.38%

Appendix Table 17. 1988 Percent normal germination - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	1705.5530	426.3883	2.1181	0.0959
Among trees within sites	41	8253.4529	201.3037	28.024	0.0001
Among samples within trees	137	983.1325	7.1761		

cv = 2.88%

Appendix Table 18. 1986 Peak value - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	122.5568	40.8523	5.44	0.0026
Among trees within sites	49	367.6737	7.5035	16.7977	0.0001
Among samples within trees	158	70.5726	0.4467		

cv = 13.28%

Appendix Table 19. 1987 Peak value - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	310.2578	51.7096	7.1102	0.0001
Among trees within sites	74	538.1702	7.2726	24.0257	0.0001
Among samples within trees	243	73.5681	0.3027		

cv = 6.92%

Appendix Table 20. 1988 Peak value - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	93.8338	23.4585	1.4379	0.2388
Among trees within sites	41	668.8877	16.3143	80.8441	0.0001
Among samples within trees	137	27.6470	0.2018		

cv = 6.19%

Appendix Table 21. 1986 Mean daily germination - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	61.6695	20.5565	10.0511	0.0001
Among trees within sites	49	100.2157	2.0452	20.4520	0.0001
Among samples within trees	158	15.8013	0.1000		

cv = 8.40%

Appendix Table 22. 1987 Mean daily germination - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	14.5794	2.4299	15.2808	0.0001
Among trees within sites	74	11.7672	0.1590	3.51	0.0001
Among samples within trees	243	11.0056	0.0453	3.5103	

cv = 4.88%

Appendix Table 23. 1988 Mean daily germination - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	3.8578	0.9645	2.1148	0.0963
Among trees within sites	41	18.6981	0.4561	28.1513	0.0001
Among samples within trees	137	2.2256	0.0162		

cv = 4.88%

Appendix Table 24. 1986 Germination value - red spruce

Source of variation	d.f.	SS	MS	F value	Pr>F
Among sites	3	4586.3799	1528.7933	6.8626	0.0006
Among trees within sites	49	10915.7379	222.7702	16.0616	0.0001
Among samples within trees	158	2191.4217	13.8697		

cv = 18.41%

Appendix Table 25. 1987 Germination value - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	9141.8798	1523.6450	7.9981	0.0001
Among trees within sites	74	14097.0740	190.5010	14.3933	0.0001
Among samples within trees	243	3216.2036	13.2354		

cv = 10.42%

Appendix Table 26. 1988 Germination value - red spruce

Source of variation	d.f.	SS	MS	F value	Pr>F
Among sites	4	2510.0751	627.5188	1.4782	0.2264
Among trees within sites	41	17405.5880	424.5265	41.9695	0.0001
Among samples within trees	137	808.1182	5.8987		

cv = 7.46%

Appendix Table 27. 1986 Leachate conductivity - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	2095.4118	698.4706	6.8512	0.0017
Among trees within sites	24	2446.7579	101.9482	14.0676	0.0001
Among samples within trees	84	608.7500	7.2470		

cv = 3.19%

Appendix Table 28. 1987 Leachate Conductivity - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	6	83113.8108	13852.1668	6.8512	0.0017
Among trees within sites	74	16881.9626	228.1338	5.0334	0.0001
Among samples within trees	204	10877.6723	45.3236		

cv = 5.75%

Appendix Table 29. 1988 Leachate conductivity - red spruce

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	1919.3749	479.8437	4.1617	0.0060
Among trees within sites	44	5073.1863	115.2997	3.8683	0.0001
Among samples within trees	147	4381.5000	29.8061		

cv = 3.81%

Appendix Table 30. 1987 Embryo length - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	4.0769	1.0196	2.4382	0.0604
Among trees within sites	46	19.2361	0.4182	82.6352	0.0001
Among samples within trees	153	0.7685	0.0050		

cv = 1.81%

Appendix Table 31. 1988 Embryo length - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	5.8308	1.9436	7.8720	0.0002
Among trees within sites	49	12.0994	0.2469	70.5429	0.0001
Among samples within trees	159	0.5616	0.0035		

cv = 1.55%

Appendix Table 32. 1987 1000-Seed weight - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	95.9380	23.9845	2.6072	0.0472
Among trees within sites	48	441.5756	9.1995	78.4940	0.0001
Among samples within trees	159	18.6325	0.1172		

cv = 3.87%

Appendix Table 33. 1988 1000-Seed weight - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	192.0895	64.0298	7.8388	0.0002
Among trees within sites	49	400.2458	8.1683	369.6055	0.0001
Among samples within trees	159	3.5075	0.0221		

cv = 1.76%

Appendix Table 34. 1987 Seedling fresh weight - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	1272.1266	318.0317	2.5381	0.0525
Among trees within sites	46	5763.9967	125.3043	7.2914	0.0001
Among samples within trees	151	2594.9478	17.1851		

cv = 16.16%

Appendix Table 35. 1988 Seedling fresh weight - balsam fir

Source of variation	d.f.	SS	MS	F value	Pr>F
Among sites	3	810.3730	270.1243	3.5856	0.0201
Among trees within sites	49	3691.4589	75.3359	25.2966	0.0001
Among samples within trees	158	470.5324	2.9781		

cv = 5.66%

Appendix Table 36. 1987 Percent normal germination - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	10095.3311	2523.8328	1.7641	0.1521
Among trees within sites	47	67241.0888	1430.6615	18.3215	0.0001
Among samples within trees	152	11869.1613	78.0866		

cv = 20.84%

Appendix Table 37. 1988 Percent normal germination - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	6050.7899	216.9300	2.8112	0.0492
Among trees within sites	48	34438.5427	717.4696	16.6464	0.0001
Among samples within trees	54	6637.5137	43.1007		

cv = 9.48%

Appendix Table 38. 1987 Peak value - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	32.1165	8.0291	1.9827	0.1126
Among trees within sites	47	190.3274	4.0495	7.7681	0.0001
Among samples within trees	152	79.2345	0.5213		

cv = 29.14%

Appendix Table 39. 1988 Peak value - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	74.5450	24.8483	3.2641	0.0293
Among trees within sites	48	365.4036	7.6126	29.3355	0.0001
Among samples within trees	154	39.9603	0.2595		

cv = 11.25%

Appendix Table 40. 1987 Mean daily germination - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	19.7449	4.9362	1.5134	0.2136
Among trees within sites	47	153.0324	3.2618	17.2762	0.0001
Among samples within trees	152	28.6921	0.1888		

cv = 20.99%

Appendix Table 41. 1988 Mean daily germination - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	1356.0214	452.0071	2.7581	0.0524
Among trees within sites	48	7866.2691	163.8860	16.9592	0.0001
Among samples within trees	154	1488.1366	9.6632		

cv = 9.42%

Appendix Table 42. 1987 Germination value - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	883.1293	220.7823	2.5247	0.0532
Among trees within sites	47	4110.1459	87.4499	14.7392	0.0001
Among samples within trees	152	920.4492	5.9372		

cv = 39.56%

Appendix Table 43. 1988 Germination value - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	1565.0082	521.6694	2.3115	0.0880
Among trees within sites	48	10832.9166	255.6858	32.4896	0.0001
Among samples within trees	152	1069.7453	6.9464		

cv = 16.80%

Appendix Table 44. 1987 Leachate conductivity - balsam fir.

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	4	26290.0488	6572.5122	6.3139	0.0004
Among trees within sites	49	51006.8436	1040.9560	50.6442	0.0001
Among samples within trees	162	3329.7928	20.5543		

cv = 3.70%

Appendix Table 45. 1988 Leachate conductivity - balsam fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	3	20902.0474	6967.3491	21.0146	0.0001
Among trees within sites	9	16245.8394	331.5477	4.1939	0.0001
Among samples within trees	159	12569.7500	79.0550		

cv = 5.32%

Appendix Table 46. 1986 Percent filled seed - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	2412.1340	2412.1340	2.4168	0.1293
Among trees within sites	34	33994.5326	998.0745	69.7515	0.0001
Among samples within trees	96	1373.6667	14.3090		

cv = 5.83%

Appendix Table 47. 1987 Percent filled seed - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	65505.7000	32752.8500	27.6053	0.0001
Among trees within sites	24	28475.2639	1186.4693	10.3583	0.0001
Among samples within trees	81	9278.0000	114.5432		

cv = 19.29%

Appendix Table 48. 1986 Percent resin filled seed - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	2820.3637	2820.3637	2.8962	0.0979
Among trees within sites	34	33110.8484	937.8235	68.5560	0.0001
Among samples within trees	96	136.6667	14.2048		

cv = 10.63%

Appendix Table 49. 1987 Percent resin filled seed - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	74111.0474	37155.5237	31.0093	0.0001
Among trees within sites	24	28679.5556	1194.9815	42.9049	0.0001
Among samples within trees	81	2256.0000	27.8519		

cv = 11.59%

Appendix Table 50. 1986 1000-Seed weight - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	3.7752	3.7752	0.5977	0.4448
Among trees within sites	34	214.7352	6.3157	51.7260	0.0001
Among samples within trees	107	13.0667	0.1221		

cv = 3.43%

Appendix Table 51. 1987 1000-Seed weight - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	53.2051	26.6026	2.5205	0.1007
Among trees within sites	25	263.8652	10.5546	158.0031	0.0001
Among samples within trees	84	5.6075	0.0668		

cv = 2.28%

Appendix Table 52. 1986 Embryo length - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	0.0092	0.0092	0.0583	0.8104
Among trees within sites	34	5.3689	0.1579	20.5076	0.0001
Among samples within trees	107	0.8279	0.0077		

cv = 2.06%

Appendix Table 53. 1987 Embryo length - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	0.2980	0.1490	0.8538	0.4378
Among trees within sites	25	4.3626	0.1745	36.3550	0.0001
Among samples within trees	84	0.4038	0.0048		

cv = 1.61%

Appendix Table 54. 1986 Fresh weight per seedling - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	46.5230	46.5230	0.2920	0.5924
Among trees within sites	34	5416.4019	159.3059	5.8589	0.0001
Among samples within trees	106	2882.1694	27.1903		

cv = 14.57%

Appendix Table 55. 1987 Fresh weight per seedling - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	474.9743	237.4872	1.8908	0.1719
Among trees within sites	25	3140.0467	125.6019	5.3796	0.0001
Among samples within trees	82	1314.5324	23.3480		

cv = 14.61%

Appendix Table 56. 1986 Percent normal germination - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	1105.7073	1105.7073	0.98	0.3286
Among trees within sites	34	38265.6970	1125.4617	16.3826	0.0001
Among samples within trees	105	7213.3333	68.6984		

cv = 29.36%

Appendix Table 57. 1987 Percent normal germination - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	3097.7997	1548.8999	0.9846	0.3876
Among trees within sites	25	39327.6218	1573.1049	26.8230	0.0001
Among samples within trees	82	4809.1020	58.6476		

cv = 14.54%

Appendix Table 58. 1986 Peak value - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	3.4642	3.4648	0.8292	0.3689
Among trees within sites	34	142.0460	4.1778	18.9987	0.0001
Among samples within trees	105	23.0846	0.2199		

cv = 29.05%

Appendix Table 59. 1987 Peak value - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	7.9602	3.9801	0.8432	0.4422
Among trees within sites	25	118.0126	4.7205	29.7074	0.0001
Among samples within trees	82	13.0305	0.1589		

cv = 14.03%

Appendix Table 60. 1986 Mean daily germination - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	2.5130	2.5130	0.9822	0.3287
Among trees within sites	34	86.9914	2.5586	16.4116	0.0001
Among samples within trees	105	16.3660	0.1559		

cv = 29.40%

Appendix Table 61. 1987 Mean daily germination - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	6.9958	3.4979	0.9799	0.3893
Among trees within sites	25	89.2408	3.5696	26.9000	0.0001
Among samples within trees	82	10.8798	0.1327		

cv = 14.52%

Appendix Table 62. 1986 Germination value - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	27.7355	27.7355	0.6710	0.4184
Among trees within sites	34	1405.3949	41.3351	18.9056	0.0001
Among samples within trees	105	229.5762	2.1864		

cv = 48.12%

Appendix Table 63. 1987 Germination Value - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	160.9505	80.4753	0.6710	0.5201
Among trees within sites	25	2998.1935	119.9277	27.4767	0.0001
Among samples within trees	82	357.9062	4.3647		

cv = 25.48%

Appendix Table 64. 1986 Leachate conductivity - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	1	942.0625	942.0625	4.3941	0.0436
Among trees within sites	34	7289.4247	214.3948	30.0004	0.0001
Among samples within trees	107	764.6667	7.1464		

cv = 3.04%

Appendix Table 65. 1987 Leachate conductivity - Fraser fir

Source of variation	d.f.	SS	MS	F	Pr>F
Among sites	2	868.7945	434.3973	1.5691	0.2281
Among trees within sites	25	6921.2819	276.8513	9.3775	0.0001
Among samples within trees	82	2420.8792	29.5229		

cv = 4.07%

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